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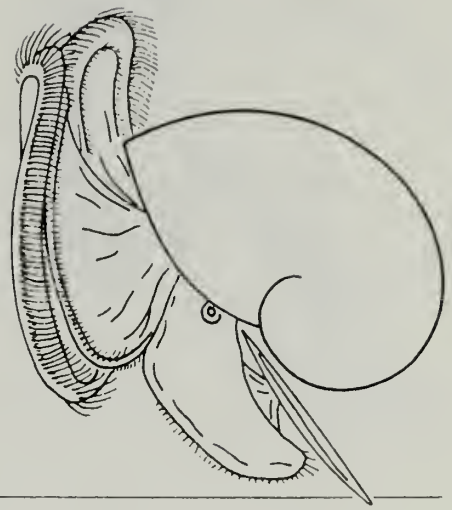

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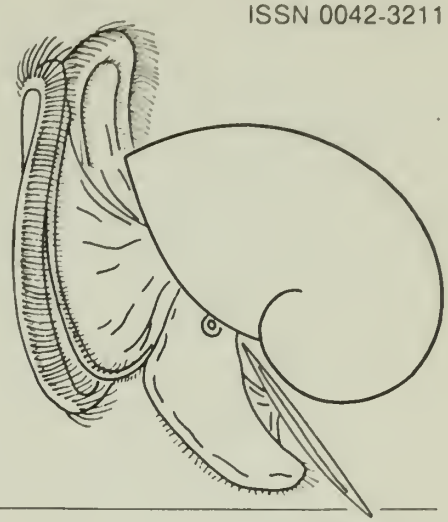

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THE VELIGER

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The Veliger is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater, or terrestrial mollusks from any region will be considered. Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimen must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

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Recent Eastern Pacific Species of the Bivalve Genus *Semele*

by

EUGENE V. COAN

Research Associate, Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.

Abstract. Twenty-eight living species-level taxa of the genus *Semele* are recognized in the eastern Pacific, including one new species from the Panamic province, ***S. jamesi***. Many type specimens are illustrated, some for the first time, and several lectotype and two neotype designations are made. A number of nominal taxa are relegated to synonymy. Each species is described and illustrated, and its distribution and habitat are discussed.

INTRODUCTION

A few years ago, I reviewed the northeastern Pacific species of the Semelidae, including that area's five species of *Semele* (COAN, 1973). I realized then that the far more diverse tropical and southern temperate eastern Pacific species of *Semele* were in even greater need of systematic attention. Indeed, I later worked out the nomenclatural confusion surrounding *S. formosa* (Sowerby) (COAN, 1983).

I have now examined the available type material of all of the Recent taxa of *Semele* from southern Alaska to southern Chile, as well as most of the available museum material, and the results are presented here.

The genus *Semele* is particularly abundant in the eastern Pacific, where 28 valid living taxa occur (Table 1). This is in contrast to only five in the western Atlantic, where the genus was well represented in the Tertiary. I have no idea why *Semele* became such a dramatic paciphile, because species of the genus occur in a variety of habitats and substrates. The western Atlantic species were most recently reviewed by BOSS (1972). They are: *Semele proficua* (Pulteney, 1799); *S. modesta* (Reeve, 1853); *S. purpurascens* (Gmelin, 1791); *S. casali* Doello-Jurado, 1949; and *S. bellestriata* (Conrad, 1837). Of these, *S. purpurascens* also occurs in the eastern Pacific. Other species are closely related to eastern Pacific taxa—*S. proficua* to *S. lenticularis* (Sowerby, 1833); *S. casali* to *S. venusta* (Reeve, 1853); and *S. bellestriata* to *S. verrucosa pacifica* Dall, 1915.

Because of their large and colorful shells, some species of *Semele* were covered in some early illustrated works, notably those of SOWERBY (1833a), REEVE (1841, 1853), and HANLEY (1857). Other nomenclaturally significant treatments of the genus, in which the many eastern Pacific taxa figure prominently, include those by SOWERBY (1833b), HANLEY (1842–1856), TRYON (1869), and LAMY (1913). These and other works with figures or of nomenclatural importance are cited in my synonymies. Not cited in the synonymies are the species lists of MÜLLER (1836:221–224), RÉCLUZ (1845:410), and D'ORBIGNY (1845:531–534), checklists for particular localities, or popular works.

Particularly significant works specifically on eastern Pacific species are those of DALL (1915), HERTLEIN & STRONG (1949), KEEN (1958, 1971), and OLSSON (1961).

FORMAT

In the following treatment, each valid taxon is followed by a synonymy, information on type specimens and type localities, notes on distribution and habitat, and additional remarks.

The synonymies include all major accounts of the species, but not minor mentions in the literature. The entries are arranged in chronological order under each species name, with changes in generic allocation from the previous entry, if any, and other notes in brackets.

The distributional information is based on specimens I have examined, except as noted. For many species, the habitat information is surprisingly sparse; depth is generally indicated on labels, but substrate type is often not. I have summarized what data I could find. Occurrences in the fossil record are taken from the literature, though occasionally questioned. The extensive fossil records for California are summarized, not cited in full.

References are provided in the Literature Cited for all works and taxa mentioned.

The following abbreviations for institutional and private collections are used in the text.

AMNH—American Museum of Natural History, New York
ANSP—Academy of Natural Sciences of Philadelphia
BM(NH)—British Museum (Natural History)
CAS—California Academy of Sciences, San Francisco
CASGTC—former numbers of the CAS Geology Type Collection
LACM—Los Angeles County Museum of Natural History
MCZ—Museum of Comparative Zoology, Harvard University
NRS—Naturhistoriska Riksmuseet, Stockholm
PRI—Paleontological Research Institution, Ithaca, New York
SBMNH—Santa Barbara Museum of Natural History
SDNHM—San Diego Natural History Museum
SUPTC—former numbers of the Stanford University Paleontology Type Collection
TU—Tulane University
UCMP—University of California at Berkeley, Museum of Paleontology
USNM—U.S. National Museum collection, in the National Museum of Natural History, Washington, D.C.
UZM—Universitetets Zoologische Museum, Copenhagen

Evans Coll.—Collection of Roger A. Evans, Redondo Beach, California
McClincy Coll.—Collection of Richard McClincy, Tucson, Arizona
Poorman Coll.—Collection of LeRoy Poorman, Westminster, California
Shy Coll.—Collection of Laura B. Shy, Seal Beach, California
Skoglund Coll.—Collection of Carol C. Skoglund, Phoenix, Arizona
Swoboda Coll.—Collection of Ed Swoboda of Beverly Hills, California

A "pair" denotes the two valves of a single individual. The term "convexity" is used here instead of "thickness" for overall shell width to prevent confusion with the thickness of shell material.

In addition to designating a number of lectotypes, I have designated two neotypes to ensure nomenclatural stability, following the guidance of ICZN Code Art. 75 and its recommendations. In some cases, type localities have been restricted, following ICZN Recommendation 72H(a)4.

I have provided coordinates for type localities and key distributional records. These are given to the nearest minute, except when more precise numbers were already available.

SYSTEMATIC ACCOUNT

SEMELIDAE Stoliczka, 1870 [1850]

Semelidae STOLICZKA, 1870:108 [1850] [as Semelinae] [Semelidae is maintained and takes precedence from Amphidesmatidae Deshayes, 1850; ICZN Code Art. 40b and Recommendation 40A].
=Amphidesmatidae DESHAYES, 1850:317–361 [as "Famille Les Amphidesmides," *ex* Latreille MS].
=Scrobiculariidae H. & A. ADAMS, 1856:408 [as Scrobiculariinae].
=Cumingiinae STOLICZKA, 1870:107.

The characteristics of the supposedly separable families Semelidae and Scrobiculariidae were reviewed by BOSS (1982:1145), who noted that there are not many significant features differentiating them. I suspect that one reason workers have not placed them together is that the less familiar name Scrobiculariidae was thought to pre-date the more familiar Semelidae. Having assured myself that this is not the case, because Semelidae takes precedence from the proposal of Amphidesmatidae in 1850, I place the scarcely distinguishable Scrobiculariidae into synonymy.

The characters that have been advanced for recognizing two families are the smooth shell of the Scrobiculariidae, the lack of lateral teeth in this family, and its smooth, homorhabdic ctenidia. However, some generic units that have traditionally remained in the Semelidae have smooth shells (*e.g., Abra, Leptomya, Theora*) and lack lateral teeth (*Thyellisca, Souleyetia*)(KEEN, 1969:635–637). The generalization about the ctenidia was made in the absence of information about most genera.

Semele Schumacher, 1817

Semele SCHUMACHER, 1817:53, 165–166; pl. 18, fig. 2.
Type species: *Tellina reticulata* SPENGLER, 1798:115, *non* LINNAEUS, 1767:1119; by monotypy; = *Tellina proficua* PULTENEY, 1799:29; pl. 5, fig. 4.—Western Atlantic.

BOSS (1972), who treated the western Atlantic species of *Semele,* provided a detailed account of morphological features of the genus and examined the anatomy of *Semele purpurascens* (Gmelin). He also reviewed previous work on the anatomy of other species of the genus, including the monograph on the Chilean *S. solida* (Gray) by SCHRÖDER (1916) but not the treatment of FISCHER (1857:334–339; pl. 13, fig. 5) on *S. proficua* (Pulteney).

The subgenera I have used under *Semele* may not represent monophyletic units, but they are convenient morphological groupings in a genus with so many species. In addition to the generic units discussed below, KEEN (1969: 636) lists *Syndesmyella* Sacco, 1901 (SACCO, 1901:122–123, 210; pl. 16, figs. 29, 30), as a synonym of *Semele,* but it appears to be more closely related to *Abra* (BOSS, 1972:8); its type species, by original designation, is *S. plioovoides* Sacco, 1901 (misspelled by both Keen and Boss as *S.* "*pliovoides*").

The word *desma* is a Greek term for "band" or "bundle" and is a neuter noun. Adjectives combined with it should have neuter endings. This is also true of words derived from it, such as *Amphidesma* ("divided ligament"). Thus, it should have been *A. solidum,* not *A. solida* as GRAY (1828) spelled it. Such incorrect terminations are to be automatically corrected (ICZN Code Arts. 31c, 32d(ii)). *Semele,* on the other hand, was based on a Greek goddess,[1] and adjectives combined with it should have feminine terminations. Thus, it should be *Semele solida* (Gray).

(*Semele*), *s.s.*

The taxa included here are mostly rounded in outline, thick-shelled, and live in shallow water in the sand matrix among rocky rubble.

Semele (*S.*) *bicolor* (C. B. Adams, 1852)

(Figures 1–3)

Amphidesma bicolor C. B. Adams, 1852: C. B. ADAMS, 1852a: 512–513, 547 [1852b:288–289, 323]; CARPENTER, 1857b: 279, 303 [*Semele*]; CARPENTER, 1864a:367 [1872:203]; CARPENTER, 1864b:543, 553, 619 [1872:29, 39, 105]; TRYON, 1869:122 [as a synonym of *S. venusta*]; LAMY, 1913:356, footnote; DALL, 1915:26; TURNER, 1956:35, 128–129; pl. 18, figs. 7, 8; KEEN, 1958:195; fig. 477; KEEN, 1971:249–250; fig. 625; BERNARD, 1983:46; GEMMELL *et al.,* 1987:54; fig. 65.

Semele fucata Mörch, 1860: MÖRCH, 1860:190; KEEN, 1966b: 12, 13, 16; fig. 16a, b [as a synonym of *S. bicolor*].

Type material and localities: *A. bicolor*—MCZ 186504, holotype, right valve; length, 20.5 mm; height, 18.6 mm; convexity, 4.9 mm [pair would be about 9.8 mm] (Figure 1). Panama, presumably near Panama City (about 8°58′N, 79°32′W); C. B. Adams, 27 Nov. 1850–2 Jan. 1851.

S. fucata—UZM [no #], lectotype (KEEN, 1966b:12), right valve; length, 13.8 mm; height, 12.1 mm; convexity, 2.8 mm [pair would be about 5.6 mm] (Figure 2). UZM, paralectotypes, 1 pair, 3 valves. [Depto.] Sonsonate, El Salvador (about 13°N, 90°W).

Description: Small (length to 31.3 mm; SBMNH 31076; Guaymas, Sonora, Mexico); rounded; equivalve; shells thin; slightly longer, rounded anteriorly; slightly truncate posteriorly; antero-dorsal margin slightly concave near beaks, with a small lunule; postero-dorsal margin straight to slightly convex, with an escutcheon, larger in left valve; posterior end slightly flexed, more evident in right valve. Periostracum thin, tan. Sculpture of concentric growth lines and fine radial striae. White externally, with dark purple umbones and a white radial patch on anterior slope of beaks; internally with a purplish suffusion; some specimens with tan flecks on postero-dorsal margin. Pallial sinuses medium in size. Hinge plate narrow.

Figure 3 depicts an adult pair from Sonora, Mexico (CAS 064674), in better condition than either of the two types.

Distribution and habitat: In the Gulf of California from Bahía Willard, Baja California Norte (29°49′N, 114°24′W) (SDMNH 90020), and Puerto Lobos, Sonora (30°13′N, 112°50′W) (CAS 064523), to Mancora, Piura Prov., Peru (4°6′S, 81°4′W) (SBMNH 34904). Most material has been obtained in beach drift. The available records indicate a habitat from the lower intertidal zone to 20 m (mean, 3 m); on sand (GEMMELL *et al.,* 1987:54). I have examined 66 lots.

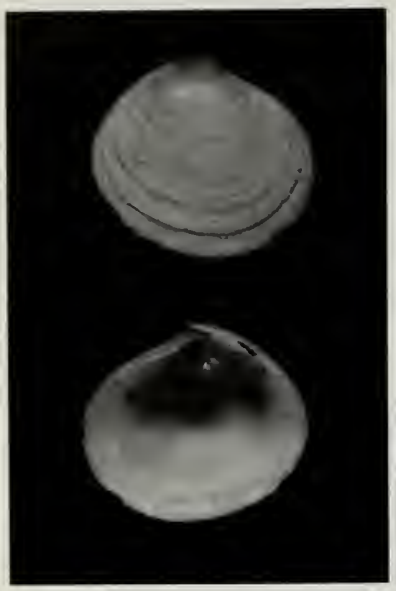
This species has been reported (as "cf.") from Pliocene strata on Isla Carmen, Baja California Sur (EMERSON & HERTLEIN, 1964:341, 350).

Table 1

The Recent eastern Pacific species of *Semele.*

Semele (*Semele*) *bicolor* (C. B. Adams, 1852)
S. (*S.*) *californica* (Reeve, 1853, *ex* A. Adams MS)
S. (*S.*) *corrugata* (Sowerby, 1833)
S. (*S.*) *decisa* (Conrad, 1837)
S. (*S.*) *elliptica* (Sowerby, 1833)
S. (*S.*) *flavescens* (Gould, 1851)
S. (*S.*) *lenticularis* (Sowerby, 1833)
S. (*S.*) *pilsbryi* Olsson, 1961
S. (*S.*) *rubropicta* Dall, 1871
S. (*S.*) *solida* (Gray, 1828)
S. (*S.*) *sowerbyi* Tryon, 1869
S. (*S.*) *tortuosa* (C. B. Adams, 1852)
S. (*Amphidesma*) *craneana* Hertlein & Strong, 1949
S. (*A.*) *formosa* (Sowerby, 1833)
S. (*A.*) *pallida* (Sowerby, 1833)
S. (*A.*) *purpurascens* (Gmelin, 1791)
S. (*A.*) *venusta* (Reeve, 1853, *ex* A. Adams MS)
S. (*Elegantula*) *rupicola* Dall, 1915
S. (*E.*) *rupium* (Sowerby, 1833)
Semele, s.l.
[group of *S. barbarae*]
S. barbarae (Boone, 1928)
S. jovis (Reeve, 1853, *ex* A. Adams MS)
S. rosea (Sowerby, 1833)
[group of *S. guaymasensis*]
S. guaymasensis Pilsbry & Lowe, 1932
S. pulchra (Sowerby, 1832)
S. verrucosa verrucosa Mörch, 1860
S. verrucosa pacifica Dall, 1915
[no group]
S. ***jamesi*** Coan, sp. nov.
S. laevis (Sowerby, 1833)

[1] Semele was the daughter of King Cadmus of Thebes. She was loved by Zeus. Hera, prompted by jealousy, persuaded Semele to ask Zeus to appear before her in all his glory. When Zeus complied, Semele was consumed by lightning, after giving birth to a son of Zeus, Dionysus, who later found Semele in Hades and took her to Olympus.



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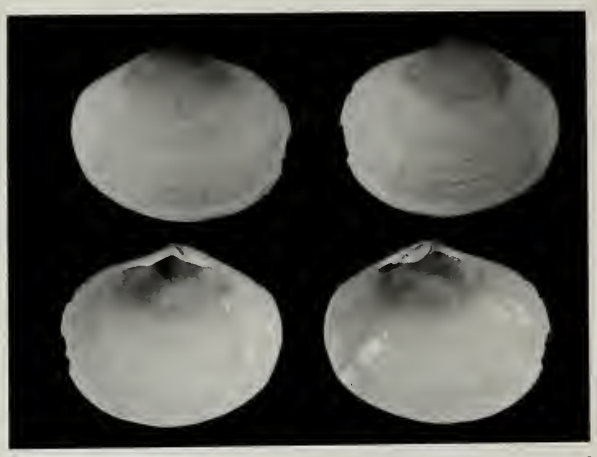

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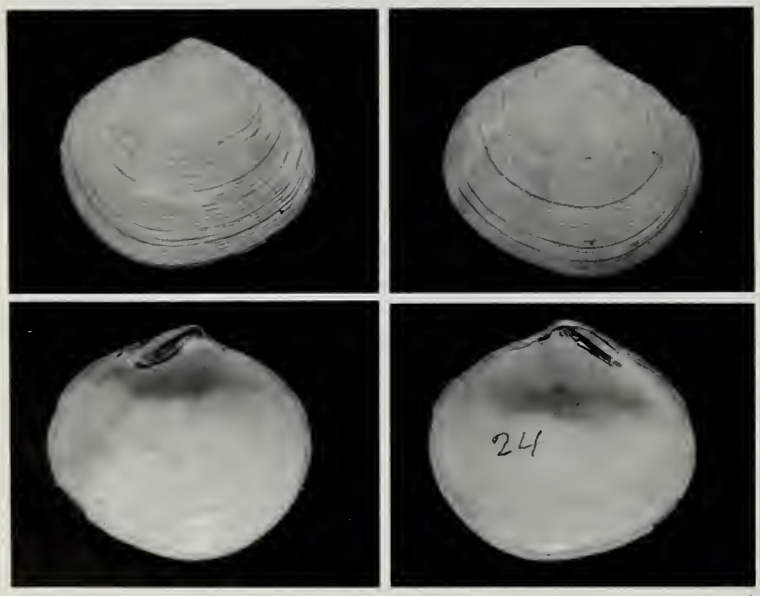

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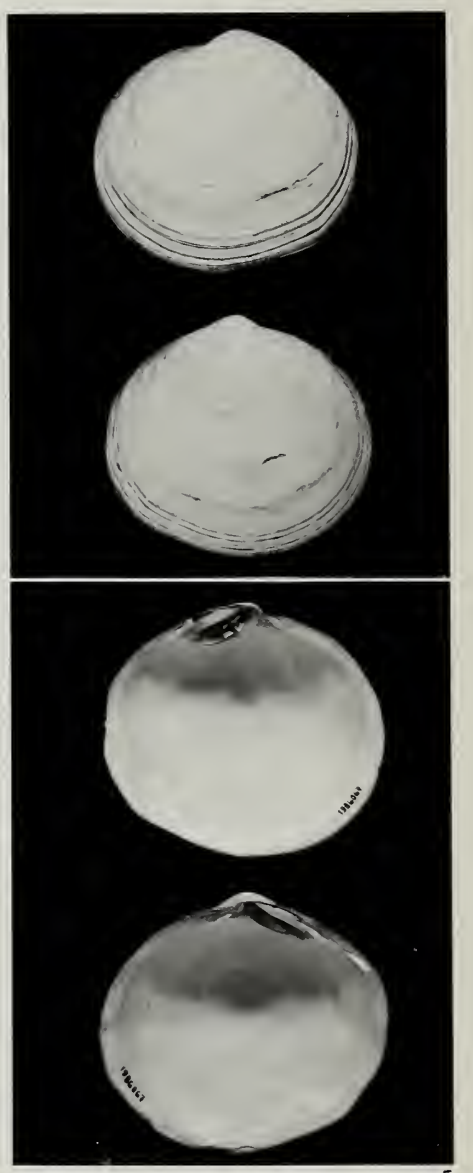

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Remarks: KEEN (1966b) showed that Mörch's *Semele fucata* is a synonym of *S. bicolor*. However, *Amphidesma striosum* and *A. ventricosum* of C. B. Adams, which she relegated to synonymy here as well, belong instead as synonyms elsewhere.

The distinctive purple color on the umbones of this species is its hallmark. This character, however, is difficult to see in faded, beachworn valves, and I have found no other character to differentiate such material from *Semele lenticularis* (Sowerby) of similar condition.

CARPENTER's (1857c:28) record of *Semele venusta* (Reeve) from Mazatlán, Sinaloa, he later decided was based on this species (CARPENTER, 1864a:367; 1864b:543, 553). Confused, TRYON (1869) synonymized the two unrelated taxa.

Semele (*S.*) *californica* (Reeve, 1853, *ex* A. Adams MS)

(Figure 4)

Amphidesma californica Reeve, *ex* A. Adams MS: REEVE, 1853:pl. 3, fig. 19 [as "A. Adams"]; A. ADAMS, 1854: 96 [*Semele*]; CARPENTER, 1857b:287, 289, 303; 1864b: 619, 665 [1872:105, 151]; TRYON, 1869:119; LAMY, 1913: 359–360; DALL, 1915:25 [as a probable synonym of *S. corrugata*]; BURCH, 1945a:18; 1945b:17; HERTLEIN & STRONG, 1949:240–241 [as a subspecies of *S. corrugata*]; KEEN, 1958:195–196; fig. 478 [as a subspecies of *S. corrugata*]; OLSSON, 1961:362 [as a synonym of *S. flavescens*]; KEEN, 1971:249–250; fig. 626; COAN, 1973: 325; BERNARD, 1983:46.

Type material and locality: BM(NH) 1986065/1, **lectotype (here designated),** the figured specimen, pair; length, 41.7 mm; height, 37.8 mm; convexity, 17.8 mm (Figure 4). BM(NH) 1986065/2, 3, paralectotypes. "Gulf of California," **here restricted to La Paz, Baja California Sur** (24°10′N, 110°19′W), Mexico.

Description: Medium-sized (length to 42.0 mm; SBMNH 34906; Bahía Magdalena, Baja California Sur); rounded; right valve slightly more inflated; shells average to heavy in thickness; approximately equilateral; rounded anteriorly; slightly truncate posteriorly; antero-dorsal margin straight to rounded, with a lunule; postero-dorsal margin rounded, with an indistinct escutcheon. Periostracum thin, brown. Sculpture of heavy, wavy concentric ribs, especially evident near ventral margin, and fine radial threads. White externally, sometimes with reddish flecks on dorsal margin and escutcheon; generally yellow to orange within, darkest along ventral margin. Pallial sinuses small. Hinge plate heavy.

Distribution and habitat: This species has a very restricted distribution in Mexico: Bahía Santa María, Baja California Sur (24°45′N, 112°15′W) (USNM 264777), into the western Gulf of California as far north as Bahía San Luis Gonzaga, Baja California Norte (29°45′N, 114°20′W) (SBMNH 34905); and in eastern Gulf on the Sonoran coast from Isla Venado (27°57′N, 111°9′W) (ANSP 354936) to Guaymas (27°50′N, 110°54′W) (LACM 124455). Nearly all the material has been collected in beach drift, but the limited data available suggest that this species nestles in rocky rubble from the low intertidal zone to 3 m. I have examined 64 lots.

A lot labeled Isla San Martín, Baja California Norte (SDNHM 91334), is probably the result of an error from the mixing of previously unnumbered material. Records of this species from California (WILLIAMSON, 1892:186; KEEP, 1904:86; 1910:97; KEEP & BAILY, 1935:107) are in error, and were perhaps based on misidentified specimens of *Semele decisa* (Conrad).

Records of this species from Japan (SCHRENCK, 1867: 569–570, 972; pl. 22, fig. 10; DUNKER, 1882:195) were probably based on specimens of *Semele cordiformis* (HOLTEN, 1803:10).

HERTLEIN & STRONG (1949:241) reported this species from strata of Pleistocene age at Bahía Magdalena, Baja California Sur, and HERTLEIN (1957:63) from similar strata on Isla Carmen, at the southern end of the Gulf of California. OLSSON (1942:10) noted it in Pleistocene deposits on the Burica Peninsula, Costa Rica (as "cf."), an improbable record.

Remarks: This species accounts for early records of the South American *Semele corrugata* (Sowerby) from Baja California (for example, STEARNS, 1894:156). HERTLEIN & STRONG (1949), followed by KEEN (1958), then made this distinctive Gulf of California species a subspecies of *S. corrugata*.

Semele (*Semele*) *corrugata* (Sowerby, 1833)

(Figures 5, 6)

Amphidesma corrugatum Sowerby, 1833: SOWERBY, 1833a:1 [7] [*nomen nudum*; cites only a figure in his unpublished "Species Conchyliorum"]; SOWERBY, 1833b:200; HANLEY, 1843:44; 6; pl. 12, fig. 21 [not pl. 12, fig. 5, which is *S. flavescens*]; 1856:341; REEVE, 1853:pl. 1, fig. 4; HANLEY, 1857:pl. 2, fig. 13; CARPENTER, 1864b:640 [1872:126] [*Semele*]; TRYON, 1869:119; DALL, 1909:271; LAMY, 1913:361–362; DALL, 1915:25; HERTLEIN & STRONG, 1949:241, footnote; OLSSON, 1961:359, 361, 537; pl. 64, fig. 1; KEEN, 1971:249–250; fig. 627; BERNARD, 1983:46.

Amphidesma croceum Gould, 1850: GOULD, 1850:218; GOULD,

←

Explanation of Figures 1 to 6

Figures 1–3. *Semele* (*S.*) *bicolor* (C. B. Adams). Figure 1: Holotype of *Amphidesma bicolor*; length, 20.5 mm. Figure 2: Lectotype of *S. fucata* Mörch; length, 13.8 mm. Figure 3: CAS 064674; Bahía Algodones, Sonora, Mexico; length, 26.0 mm.

Figure 4. *Semele* (*S.*) *californica* (Reeve). **Lectotype** (herein) of *Amphidesma californica*; length, 41.7 mm.

Figures 5 and 6. *Semele* (*S.*) *corrugata* (Sowerby). Figure 5: **Lectotype** (herein) of *Amphidesma corrugatum*; length, 89.5 mm. Figure 6: Holotype of *A. croceum* Gould; length, 83.0 mm.

1852:399; 1860:pl. 35, figs. 512a, b; 1862:78, 246; TRYON, 1869:119 [*Semele*]; LAMY, 1913:361, footnote; DALL, 1915:25 [as a synonym of *S. solida*]; JOHNSON, 1964:62; BERNARD, 1983:47 [as a synonym of *S. solida*].

Semele solida (Gray), *auctt., non* Gray, 1828: DALL, 1909: 294; pl. 28, fig. 10.

[*non* GRAY, 1828:6].

Type material and localities: *A. corrugatum*—BM(NH) 1986067, **lectotype (here designated),** the specimen figured by REEVE (1853), pair; length, 89.5 mm; height, 81.4 mm; convexity, 46.2 mm (Figure 5). BM(NH) 1986066, paralectotype, the syntype measured by Sowerby, pair; length, 53.1 mm; height, 48.6 mm; convexity, 25.0 mm. BM(NH) 1986068/1, 2, additional paralectotypes. "Peru and Iquique," 18 m, coarse gravel; H. Cuming, 1828–1830. These specimens probably came from Peru; I have not seen this species from as far south as Iquique, Tarapaca Prov., Chile. **I here restrict the type locality to Paita, Piura Prov., Peru** (5°5′S, 81°7′W), where the species is present (USNM 48451).

A. croceum—USNM 5899, holotype, pair; length, 83.0 mm; height, 75.1 mm; convexity, 40.0 mm (Figure 6). "Callao?," Lima Prov., Peru (12°3′S, 77°10′W); U.S. Exploring Expedition, June–July 1839 (TYLER, 1968:74–77).

Description: Large (length to 97.8 mm; ANSP 275950; Laguna Grande, Ica Prov., Peru); right valve decidedly more inflated; shells heavy; approximately equilateral to longer anteriorly; rounded anteriorly; slightly truncate posteriorly; antero-dorsal margin concave near beaks, convex anteriorly, with a slight lunule; postero-dorsal margin straight, slightly convex, with a slight escutcheon in left valve. Periostracum straw-colored to dark brown, present only as ventral shreds in adult. Sculpture of thin concentric ribs, which are strongest anteriorly and fade out toward posterior slope, and fine radial threads. White externally; internally generally bright orange or yellow (occasionally white), with a purplish stain at ends of hinge. Pallial sinuses large. Anterior lateral tooth in right valve small, not projecting ventrally.

Distribution and habitat: Santa Elena, Guayas Prov., Ecuador (2°12′S, 80°52′W) (HOFFSTETTER, 1952:41, as "*S. solida*"; OLSSON, 1961; I have not seen specimens from this far north but find little reason to doubt these records); between El Rubio and Punto Mero, Piura Prov., Peru (3°54′S, 80°53′W) (LACM 72-85, 2 juveniles); Negritos, Piura Prov., Peru (4°40′S, 81°19′W) (OLSSON, 1961); Punta Parinas, Piura Prov., Peru (4°40′S, 81°20′W) (USNM 424414), to Laguna Grande, Bahía de Independencia, Ica Prov., Peru (14°8′S, 76°15′W) (USNM 537934, 537942; LACM 72-77; SBMNH 34907, 34908; ANSP 275950, 300982). Depth records are from the intertidal zone to 9 m (mean, 5 m). The only substrate types noted on labels are in sand or among rocks. I have examined 49 lots.

STEARNS (1891:313), repeated by DALL (1909:271), reported this species from the Gulf of Panama, but there is no material in any collection to support this unlikely record. Reports of it from Baja California (STEARNS, 1894: 156) were based on specimens of *Semele californica* (Reeve). HERTLEIN & STRONG's (1955a:123) record of it from Isla Baltra in the Galápagos Islands was based on a specimen of *S. flavescens* (Gould) (CAS 064672).

One specimen labeled as coming from Valparaiso, Chile (USNM 73492), is probably mislabeled and may also account for OLSSON's (1961) Chilean record. GIGOUX (1935: 284) reported this species from Atacama Prov., Chile, and HUPÉ, in Gay (1854:360), reported it from "Valparaiso, etc."; I suspect that these records were based on specimens of *Semele solida* (Gray). SOOT-RYEN's (1959:63–64) records of this species from southern Chile were based on specimens of *S. solida* that I have examined (NRS).

LAMY (1910:C90) reported this species as a subfossil at Paita, Peru, which may be correct, and I suspect that HOFFSTETTER's (1948:80) record of *Semele solida* from Pleistocene strata on the Santa Elena Peninsula, Ecuador, is really *S. corrugata,* as may be BOSWORTH's (1922:178) record from Pleistocene strata at Lobitos, Piura Prov., Peru.

Remarks: This species is easily confused with *Semele solida* (Gray). The latter has a more southern distribution, the two overlapping between Callao and Bahía Independencia, Peru. *Semele corrugata* (1) attains a larger size; (2) is often yellow or orange within; (3) is more inequivalve, with the right valve conspicuously more inflated; (4) is often less equilateral, being longer anteriorly (*S. solida* is generally equilateral); (5) has more subdued concentric sculpture on the posterior slope (in *S. solida,* it is subdued on the anterior slope instead); (6) has a smaller, more horizontally directed anterior lateral tooth in the right valve (in *S. solida,* it is larger and more ventrally directed); and (7) has a smaller lunule.

Some authors have synonymized *Amphidesma croceum* with *Semele solida,* but it belongs here.

Semele (*Semele*) *decisa* (Conrad, 1837)

(Figures 7, 8)

Amphidesma decisum Conrad, 1837: CONRAD, 1837:239; pl. 19, fig. 2 [as "*A. decisa*"]; HANLEY, 1843:44–45; 7; pl. 12, fig. 52; 1856:341; REEVE, 1853:pl. 4, fig. 24; CARPENTER, 1857a:213 [*Semele*]; 1857b:195, 228, 231, 303, 351; 1864b:536, 540, 640 [1872:22, 36, 126]; TRYON, 1869:119; ARNOLD, 1903:165–166; LAMY, 1913:357–358; DALL, 1915:25; I. OLDROYD, 1925:179; GRANT & GALE, 1931:376, 908; pl. 14, figs. 13a, b; BURCH, 1945a: 17, 19 (fig.); 1945b:17; HERTLEIN & STRONG, 1949: 239, 242; KEEN, 1966a:171; COAN, 1973:316–318; figs. 1, 2, 14; BERNARD, 1983:46.

Amphidesma rubrolineatum Conrad, 1837 [first revision: COAN (1973)]: CONRAD, 1837:239; pl. 18, fig. 11 [as "*A. rubrolineata*"]; HANLEY, 1843:44; 7; pl. 12, fig. 51; 1856:341; CARPENTER, 1857a:212 [*Semele*]; 1857b:163, 195, 232, 303, 351; 1864b:536, 640 [1872:22, 126] [as a possible synonym of *S. decisa*]; TRYON, 1869:122; DALL, 1871:

144; LAMY, 1913:363–364, footnote; DALL, 1915:27–28; KEEN, 1966a:171; COAN, 1973:316 [as a synonym of *S. decisa*].

?*Semele rubrotincta* Carpenter, *ex* "Conrad" MS [*nomen nudum*; probably a misspelling of *S. rubrolineata*]: CARPENTER, 1857b:284, 352 [*nomen nudum*]; DALL, 1915: 27.

?*Semele* "*californica* Conrad," *auctt.*, ?error for *S. decisa* (Conrad): KEW, 1924:88.

Semele "*dehiscens*," *auctt.*, misspelling of *S. decisa*: HARTMAN, 1963:88, 187.

Type material and localities: *A. decisum*—BM(NH) 1861.5.20.137, lectotype (COAN, 1973:316), pair; length, 48.1 mm; height, 44.0 mm; convexity, 21.0 mm (Figure 7). Conrad's stated length of 127 mm would be larger than any known specimen and was probably in error. According to S. Morris (in correspondence, 13 June 1986), there was probably at least one other syntype; thus my calling this one a "holotype" in 1973 (COAN, 1973) constitutes a lectotype designation (ICZN Code Art. 74b). "In the vicinity of" San Diego, San Diego Co., California (approx. 32°42′N, 117°16′W); "in deep water"; T. Nuttall; 15 April–8 May 1836 (GRAUSTEIN, 1967:313–317).

A. rubrolineatum—Original lost (CARPENTER, 1864b:640; KEEN, 1966a:171). USNM 590481, **neotype (here designated),** pair; length, 25.7 mm; height, 22.3 mm; convexity, 9.4 mm (Figure 8). USNM 665764, 3 pairs, 1 valve from the same lot. Original locality same as *A. decisum*. The neotype is from Mission Bay, San Diego Co., California (32°44′N, 117°14′W); W. K. Emerson; 11 Nov. 1946. A neotype is designated because the early date of this *nomen dubium* threatens nomenclatural stability. Conrad's figure is not as good as one would like, but it was probably based on a young specimen of *S. decisa* not unlike the neotype selected.

Description: Large (length to 119.2 mm; Evans Coll., cited by DRAPER, 1987:38; Laguna Bay, Orange Co., California); rounded; right valve more inflated; shells average in thickness; slightly longer, rounded anteriorly; truncate posteriorly; antero-dorsal margin slightly concave, with a weak lunule; postero-dorsal margin straight, with an escutcheon (which may become obscure in large specimens). Periostracum light to dark tan, often present only as ventral shreds. Sculpture of heavy, irregular concentric folds and fine radial threads. White to tan externally; white internally, with purplish stains, especially on margins; hinge stained purple. Pallial sinuses medium in size.

KELLOGG (1915:658, 660; fig. 32) illustrated its ciliary currents.

Distribution and habitat: Point Arguello, Santa Barbara Co., California (34°34′38″N, 120°38′59″W) (CAS 064541), to Punta Entrada, Bahía Magdalena, Baja California Sur (24°32′N, 112°4′W) (LACM 71-14); ?Cabo San Lucas, Baja California Sur (22°52′N, 109°53′W) (CAS 064525, AMNH 78436, representing a single sample and not verified in recent years). Depth records are from the intertidal zone to 46 m (mean, 5 m), buried in sandy rubble. I have examined 137 lots.

A lot labeled "Paso Robles" (LACM 57175), an inland town in San Luis Obispo Co., suggests a possible occurrence as far north as that county (approx. 35°38′N), but no reliable records confirm its occurrence there. A lot labeled "Puerto Peñasco," Sonora (MCZ 233099), undoubtedly represents a labeling error, as probably does a lot labeled "Mazatlán," Sinaloa (CAS 064524).

This species has been recorded by various authors from many localities in strata of late Pleistocene age from Tomales Bay, Marin Co., California (ADDICOTT, 1966:14, who summarizes previous records there), to Bahía Magdalena, Baja California Sur (JORDAN, 1936:112). It is also known from early Pleistocene strata in southern California (for example, ARNOLD, 1903; DELONG, 1941:244; CLARK, in Natland, 1957:pl. 2) and from Pliocene deposits of the Los Angeles basin (for example, WILLETT, 1946:29).

Remarks: CARPENTER (1857a:212; 1857b:163, 195, 232), following the advice of Hugh Cuming, suggested that *Amphidesma simplex* Adams & Reeve, 1850 (ADAMS & REEVE, 1850:81; pl. 20, fig. 11), described from the "Sooloo Sea," might actually be from California and be a synonym of *A. rubrolineatum* Conrad, 1837. However, the original figure of *A. simplex* and a photograph of the three syntypes in the BM(NH) show that the shells of this species are more elongate, and they were described as being golden within. Thus, there is no reason to doubt that *A. simplex* is an Asian taxon.

CARPENTER (1857a:213) repeated a suggestion of Gould that *Semele decisa* might prove to be a synonym of *S. rosea* (Sowerby). Later, CARPENTER (1857b:195, 228) decided that this was incorrect, calling this concept "Gld. (not Sow.)."

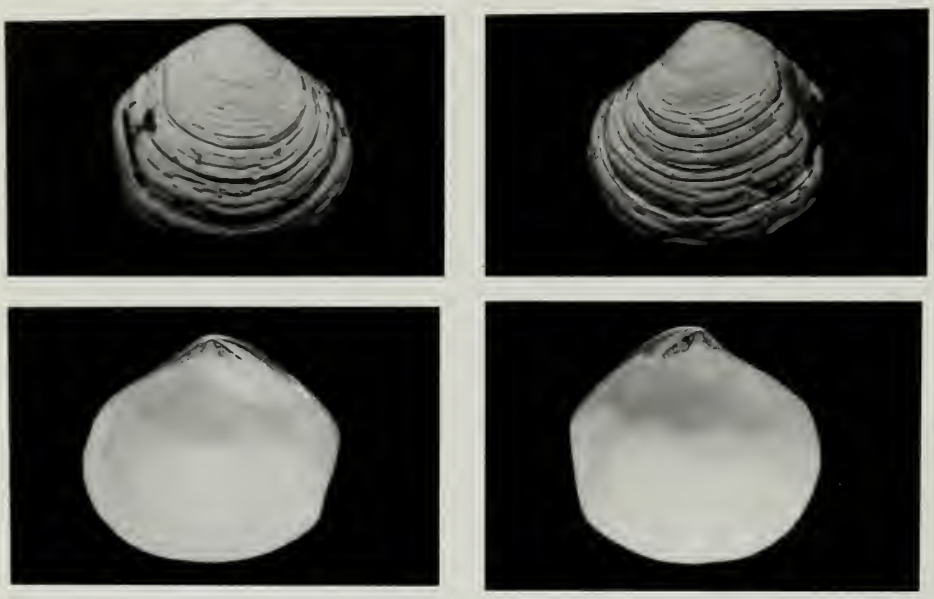
Semele (*Semele*) *elliptica* (Sowerby, 1833)

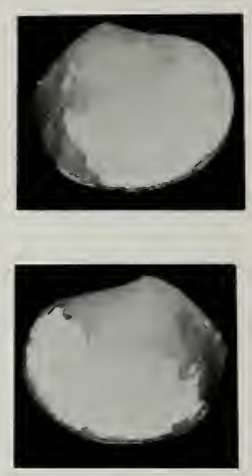
(Figure 9)

Amphidesma ellipticum Sowerby, 1833: SOWERBY, 1833a:1 [7] [*nomen nudum*; cites only a figure in his unpublished "Species Conchyliorum"]; SOWERBY, 1833b:200; HANLEY, 1843:45; C. B. ADAMS, 1852a:513 [1852b: 289]; REEVE, 1853:pl. 5, fig. 31; CARPENTER, 1857b: 279, 303 [*Semele*]; 1857c:28; HANLEY, 1857:pl. 2, fig. 12; CARPENTER, 1864a:367 [1872:203]; CARPENTER, 1864b:553 [1872:39]; TRYON, 1869:120; DALL, 1909: 271; LAMY, 1913:262–263; DALL, 1915:26; KEEN, 1958: 196–197; fig. 480; OLSSON, 1961:359, 362, 537; pl. 64, fig. 5; CAUQUOIN, 1969:574; KEEN, 1971:249–250; fig. 629; BERNARD, 1983:46.

[Not to be confused with *A. ellipticum* KOCH & DUNKER, 1837:19, 64; pl. 1, fig. 3, an unrelated fossil taxon.]

Type material and locality: BM(NH) 1986070/1, **lectotype (here designated),** the figured syntype, pair; length, 58.9 mm; height, 50.8 mm; convexity, 25.0 mm (Figure 9). BM(NH) 1986070/2, 3, paralectotypes. "Monte Christe" [Montecristi, inland from Manta], Manabi Prov.,





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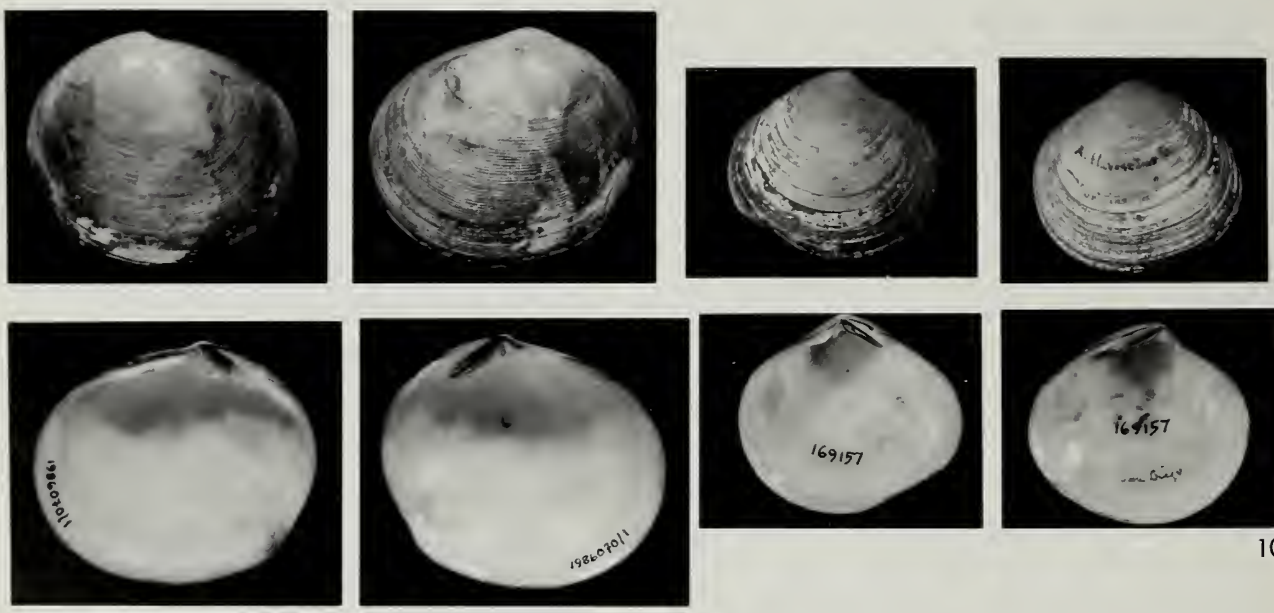

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"W. Col." [Ecuador] (0°57′S, 80°44′W), 16 m, sandy mud; H. Cuming, 1828–1830.

Description: Medium-sized (to 75.5 mm; SDNHM 15840; Panama); elliptical; equivalve; shells average in thickness; much longer, rounded anteriorly; somewhat truncate posteriorly; antero-dorsal margin slightly rounded, with an elongate lunule; postero-dorsal margin slightly rounded, with a narrow escutcheon. Periostracum olive-brown, strongly adherent. Concentric sculpture regular, subdued, almost smooth in young specimens, then grooved, then of low, broad ribs. Shell white externally; internally white, sometimes with a pink flush; beaks white. Pallial sinuses small.

Distribution: Jiquilillo, Chinandega Depto., Nicaragua (13°N, 87°W) (LACM 86-267.1), to Punta Santa Elena, Guayas Prov., Ecuador (2°12′S, 80°58′W) (CAS 064526). Peña (1971:136) reported it from Puerto Pizarro, Tumbez Prov., Peru (3°29′S, 80°23′W), and this may be correct. It has been recorded only from the intertidal zone; the few habitat records indicate mud, sand, and rock substrates. I have examined 53 lots.

What was recorded by Parker (1964a:161) as this species from the Playa Novillero area, Nayarit, Mexico, proves to be specimens of *Semele pallida* (Sowerby) (MCZ 260379, 260386). What was reported by Soot-Ryen (1959:63) as this species from Iquique, Chile, is young *S. solida* (Gray) (NRS).

Hoffstetter (1948:80; 1952:41) reports this species from Pleistocene strata on the Santa Elena Peninsula, Ecuador, which is probably correct. Herm (1969:120) reports it from upper and middle Pleistocene strata in Chile, records that I regard with some doubt.

Semele (*S.*) *flavescens* (Gould, 1851)

(Figures 10, 11)

Amphidesma flavescens Gould, 1851: Gould, 1851:89–90; Gould, 1853:392–393; Gould & Carpenter, 1857: 199 [*Semele*]; Carpenter, 1857a:548; 1857b:226, 231, 245, 279, 289, 303, 351 [misspelled as "*flavicans*" on pp. 231, 279, 289]; Carpenter, 1857c:548; Gould, 1862:211–212; Carpenter, 1864a:367 [1872:203]; Carpenter, 1864b:542, 553, 562, 619 [1872:29, 39, 48, 105]; Tryon, 1869:120; Lamy, 1913:358–359; Dall, 1915:25; I. Oldroyd, 1925:182; Grant & Gale, 1931: 376; Burch, 1945a:17; 1945b:17; Hertlein & Strong, 1949:240, 242–243; Durham, 1950:90, 169, 170; pl. 24, fig. 2; pl. 25, fig. 10; Keen, 1958:196–197; fig. 481; Olsson, 1961:359, 362–363, 537; pl. 64, figs. 4, 4a, 4b; Johnson, 1964:77; pl. 29, fig. 7; Cauquoin, 1969:575; Keen, 1971:249–251; fig. 630; Coan, 1973:325; Bernard, 1983:46; Gemmell *et al.*, 1987:55; figs. 66, 67.

Amphidesma proximum C. B. Adams, 1852: C. B. Adams, 1852a:513–514, 547 [1852b:289–290, 323]; Reeve, 1853: pl. 3, fig. 20; Hanley, 1843:341–342; Gould & Carpenter, 1857:199; Carpenter, 1857b:226, 231, 245, 279, 289, 303 [*Semele*]; Carpenter, 1857c:28, 548; Carpenter, 1864a:367 [1872:203] [as a synonym of *S. elliptica*]; Carpenter, 1864b:553, 576, 668 [1872:39, 62, 154] [as a probable synonym of *S. elliptica*]; Tryon, 1869:120 [as a synonym of *S. elliptica*]; Lamy, 1913:359 [as a synonym of *S. elliptica*]; Dall, 1915:25 [as a synonym of *S. flavescens*]; Turner, 1956:76–77, 128–129; pl. 18, figs. 14, 15.

Amphidesma corrugatum Sowerby, *auctt., non* Sowerby, 1833: Hanley, 1843:6; pl. 12, fig. 5; 1856:341 [says fig. was *S. proxima*].

[*non* Sowerby, 1833b:200].

Semele "*flavicans*," *auctt.*, misspelling of *S. flavescens*: Carpenter, 1857b:231, 279, 289; Dall, 1871:145.

Semele "*flavencens*," *auctt.*, misspelling of *S. flavescens*: Olsson, 1932:127.

Type material and localities: *A. flavescens*—MCZ 169157, lectotype (Johnson, 1964:77, as "holotype"—ICZN Code Art. 74b), pair; length, 58.0 mm; height, 52.8 mm; convexity, 28.0 mm (Figure 10). "San Diego, California" [in error]; T. P. Green. This specimen undoubtedly came from the Panamic province, and **I here correct the type locality to Guaymas, Sonora** (27°55′N, 110°53′W), where Green collected many other species (Carpenter, 1857b:231–234) and where this species is common.

A. proximum—MCZ 186563, lectotype (Turner, 1956: 128), pair; length, 44.6 mm; height, 42.0 mm; convexity, 20.2 mm (Figure 11). Panama, presumably from near Panama City (about 8°58′N, 79°32′W), reef at low tide; C. B. Adams, 27 Nov. 1850–2 Jan. 1851.

Description: Medium-sized (length to 69.0 mm; SBMNH 34909; Isla Santa Margarita, Baja California Sur); oval; equivalve; average in thickness to heavy; longer, rounded anteriorly; somewhat truncate posteriorly; antero-dorsal margin concave, with a small lunule; postero-dorsal margin straight, with a conspicuous escutcheon. Periostracum olive. Sculpture of thin, irregular concentric ribs and radial striae. White externally; white internally, sometimes with a yellowish or cream-colored hue (hence the name). Pallial sinuses medium in size.

Distribution and habitat: Isla Magdalena, Baja California Sur (24°35′N, 112°5′W) (LACM 67-70; CAS 055811), into and throughout the Gulf of California, to Negritos, Piura Prov., Peru (4°40′S, 81°19′W) (USNM 359655). Grant & Gale (1931:376) cite a specimen from Laguna Ojo de Liebre (Scammon's), on the outer coast of Baja California (27°50′N, 114°15′W), but it cannot be located

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Explanation of Figures 7 to 11

Figures 7 and 8. *Semele* (*S.*) *decisa* (Conrad). Figure 7: Lectotype of *Amphidesma decisum*; length, 48.1 mm. Figure 8: **Neotype** (herein) of *A. rubrolineatum* Conrad; length, 25.7 mm.

Figure 9. *Semele* (*S.*) *elliptica* (Sowerby). **Lectotype** (herein) of *Amphidesma ellipticum*; length, 58.9 mm.

Figures 10 and 11. *Semele* (*S.*) *flavescens* (Gould). Figure 10: Lectotype of *Amphidesma flavescens*; length, 58.0 mm. Figure 11: Lectotype of *A. proximum* C. B. Adams; length, 44.6 mm.

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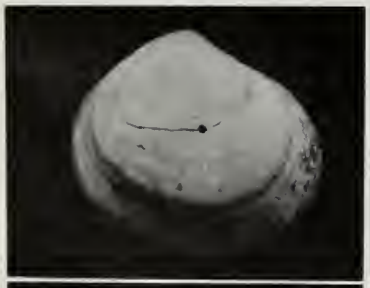

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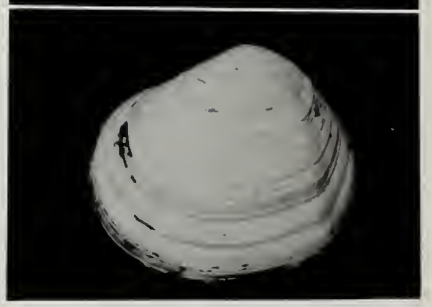

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for verification at the CAS (present home of the Stanford University collection). Single, worn valves of this species account for the records of *Semele solida* (Gray) from Tagus Cove, Isla Isabela (PILSBRY & VANATTA, 1902:549) (CAS 064527), and of *S. corrugata* (Sowerby) from Isla Baltra (HERTLEIN & STRONG, 1955a:123) (CAS 064672), Galápagos Islands, Ecuador. These are the only Galápagos records of this generally common species, and it may not be established there. Intertidal zone to 5 m (mean, 2 m), in rubble mixed with sand. It is the most common eastern Pacific *Semele*; I have examined 211 lots.

There are a number of records in Pleistocene strata: Bahía Tortugas (CHACE, 1956:178; EMERSON *et al.*, 1981: 110) and Bahía Magdalena (JORDAN, 1936:112; HERTLEIN & STRONG, 1949:243) on the outer coast of Baja California; Isla Carmen and Bahía Santa Inez (HERTLEIN, 1957:63); Isla Coronados (EMERSON & HERTLEIN, 1964: 340, 350); and Puerto Peñasco (HERTLEIN & EMERSON, 1956:165) in the Gulf of California. BARKER (1933:89) and HOFFSTETTER (1948:80) recorded it from Pleistocene strata on the Santa Elena Peninsula, Ecuador. RANSON (1959:74) reports it from raised beaches [?Pleistocene] at "Guadalupito," a little north of Chimbote, in either Ancash or La Libertad Prov., Peru, some 600 km south of its present most southerly occurrence. Pliocene records are those of EMERSON & HERTLEIN (1964:341, 350, as "cf.") at Isla Carmen in the Gulf of California and WOODRING *et al.* (1941:opp. p. 78, with question) from the San Joaquin formation in central California. OLSSON (1932:127) reports a specimen that might be allied to *Semele flavescens* in the Miocene of Peru.

Remarks: OLSSON (1961:362) incorrectly placed the distinct *Semele californica* in synonymy here.

Semele (*S.*) *lenticularis* (Sowerby, 1833)

(Figures 12–14)

Amphidesma lenticulare Sowerby, 1833: SOWERBY, 1833a:8; pl. 19, fig. 9; SOWERBY, 1833b:200; HANLEY, 1843:44; 7; pl. 12, fig. 49; 1856:341; REEVE, 1853:pl. 6, fig. 39; HANLEY, 1857:pl. 3, fig. 34; TRYON, 1869:121 [*Semele*]; DALL, 1909:272; OLSSON, 1961:359, 363–364, 538, 539; pl. 65, figs. 8, 8a, 8b; pl. 66, fig. 9; KEEN, 1971:251–252; fig. 636; BERNARD, 1983:46; GEMMELL *et al.*, 1987: 14, 56.

Amphidesma ventricosum C. B. Adams, 1852: C. B. ADAMS, 1852a:516, 547 [1852b:292, 323]; CARPENTER, 1857b: 280, 303 [*Semele*]; CARPENTER, 1864a:367–368 [1872: 203–204]; CARPENTER, 1864b:553 [1872:39]; TRYON, 1869:122; LAMY, 1913:330; KEEN, 1958:200–201; fig. 502; OLSSON, 1961:363 [as a synonym of *S. lenticularis*]; TURNER, 1965:97, 130–131; pl. 19, figs. 9, 10; KEEN, 1971:250 [as a synonym of *S. bicolor*].

Type material and localities: *A. lenticulare*—BM(NH) 1986075, holotype, pair; length, 22.4 mm; height, 20.9 mm; convexity, 11.1 mm (Figure 12). Santa Elena, Guayas Prov., "W. Col." [Ecuador] (2°11′S, 80°52′W), 11 m, sandy mud; H. Cuming, 1828–1830.

A. ventricosum—MCZ 186364, holotype, left valve; length, 15.9 mm; height, 14.9 mm; convexity, 4.5 mm [pair would be about 9 mm] (Figure 13). Panama, presumably from near Panama City (about 8°58′N, 79°32′W); C. B. Adams, 27 Nov. 1850–2 Jan. 1851.

Description: Small (to 30.3 mm; Skoglund Coll.; Puerto Lobos, Sonora, Mexico), larger in northern portion of its occurrence; rounded, southern populations proportionately higher; approximately equivalve; shells thin; anterior end longer, rounded; posterior end slightly truncate; anterodorsal margin slightly concave, with a lunule; posterodorsal margin straight, with a scarcely evident escutcheon. Periostracum thin, tan. Sculpture of faint concentric and radial threads. White externally, often with reddish flecks or chevrons on dorsal margin; white internally, sometimes with a light yellow suffusion. Pallial sinuses medium in size.

I have illustrated a large, elongate specimen from the Gulf of California (CAS 064539) (Figure 14).

Distribution and habitat: Cabo San Lucas, Baja California Sur (22°52′N, 109°53′W) (USNM 3971), into and throughout the Gulf of California, to near El Rubio and Punta Mero, Tumbes Prov., Peru (3°54′S, 80°53′W) (LACM 72-85; SBMNH 34910). Intertidal zone to 44 m (mean, 6 m), probably in rubble with a sandy matrix; on a sand bar (VOKES & VOKES, 1962:61–62). I have examined 140 lots.

Remarks: This is a fairly common but poorly understood species, frequently having been mistaken for small *Semele flavescens* (Gould), from which it can be differentiated by its thinner shells and lack of a conspicuous escutcheon. OLSSON (1961) correctly synonymized *Amphidesma ventricosum* with *S. lenticularis*, but not in lumping *S. bicolor* and *A. striosum* here as well. Although OLSSON (1961) labeled one of his figures (pl. 66, fig. 9) as "*Semele lenticulare* . . . (*bicolor*)," this specimen is typical *S. lenticularis* (PRI 25844).

SMITH (1890:301–302) synonymized *Semele lenticularis* with *S. cordiformis* (HOLTEN, 1802:10), a distinct Asian species with heavier shells and stronger radial ribs. No one else has followed this ambitious lumping.

←

Explanation of Figures 12 to 18

Figures 12–14. *Semele* (*S.*) *lenticularis* (Sowerby). Figure 12: Holotype of *Amphidesma lenticulare*; length, 22.4 mm. Figure 13: Holotype of *A. ventricosum* C. B. Adams; length, 15.9 mm. Figure 14: CAS 064539; Puerto Lobos, Sonora, Mexico; length, 30.3 mm.

Figure 15 and 16. *Semele* (*S.*) *pilsbryi* Olsson. Figure 15: Holotype of *S. pilsbryi*; length, 45.9 mm. Figure 16: SBMNH 34902; Barra de Navidad, Jalisco, Mexico; length, 40.0 mm.

Figures 17 and 18. *Semele* (*S.*) *rubropicta* Dall. Figure 17: Lectotype of *S. rubropicta*; length, 39.9 mm. Figure 18: CAS 064531; Crofton, British Columbia; length, 42.5 mm.

As Olsson (1961) first suggested, this eastern Pacific species is closest to the type species of *Semele, S. proficua* (Pulteney, 1799), which occurs from Beaufort, North Carolina, to the Golfo de San Jorge, Argentina, in the intertidal zone to 55 m (Boss, 1972:8–13). *Semele proficua* is larger, heavier, more rounded, and has heavier sculpture. Stanley (1970:176–177; pl. 30, figs. 6–9) provided information about the habitat and behavior of *S. proficua,* and Fischer (1857:335–339; pl. 13, fig. 5) described its anatomy. It is known with certainty from formations as old as the Pliocene in the western Atlantic.

Semele (*S.*) *pilsbryi* Olsson, 1961

(Figures 15, 16)

Semele pilsbryi Olsson, 1961: Olsson, 1961:360, 368, 538; pl. 65, figs. 6, 6a; Keen, 1971:253–254; fig. 640; Bernard, 1983:47.

Type material and locality: ANSP 218959, holotype, left valve; length, 45.9 mm; height, 42.4 mm; convexity, 10.0 mm [pair would be about 20 mm] (Figure 15). Bucaro, Azuero Peninsula, Los Santos Prov., Panama (about 7°25′N, 80°10′W).

Description: Medium-sized (length to 53.7 mm; LACM 68-41; Bahía Cuastocomate, Jalisco, Mexico); trapezoidal; right valve slightly more inflated; shells average in thickness; much longer, rounded anteriorly; rounded, slightly truncate posteriorly; antero-dorsal margin straight, with a small lunule; postero-dorsal margin straight, with a large escutcheon. Periostracum thin, olive to dark. Sculpture of concentric growth lines and conspicuous radial striae, which are heavier in some specimens than in others. White externally, with reddish flecks along dorsal margin; dark orange within, with purple on ends of hinge. Pallial sinuses medium in size.

I have illustrated here both right and left valves of material from Jalisco, Mexico (SBMNH 34902) (Figure 16).

Distribution and habitat: Guaymas, Sonora, Mexico (27°50′N, 110°54′W) (Shy Coll.), to Isla la Plata, Manabi Prov., Ecuador (1°15′S, 81°4′W) (SBMNH 34911). From the intertidal zone to 18 m (mean, 11 m). The only substrate noted on labels is gravel. I have examined only 6 lots, representing 5 stations.

Semele (*S.*) *rubropicta* Dall, 1871

(Figures 17, 18)

Semele rubropicta Dall, 1871: Dall, 1871:144–145, 160; pl. 14, fig. 10; Lamy, 1913:363; Dall, 1915:26; I. Oldroyd, 1924:56, 212; pl. 22, fig. 10; I. Oldroyd, 1925:180; pl. 43, fig. 10; Dall, 1925:26, 37; pl. 18, figs. 1, 2; Grant & Gale, 1931:376; Burch, 1945a:17; 1945b:17; 1945c: 30; Hertlein & Grant, 1972:300; pl. 48, figs. 1, 2, 7, 11; Coan, 1973:318–319; figs. 4, 15; Bernard, 1983: 47.

Semele rubrolineata Conrad, *auctt., non* Conrad, 1837: Carpenter, 1864b:627 [1872:113].

[*non* Conrad, 1837:239; pl. 18, fig. 11—see under *S. decisa*].

Semele ashleyi Hertlein & Grant, 1972: Hertlein & Grant, 1972:299–300; pl. 48, figs. 3, 4, 6, 9, 10.

Type material & localities: *S. rubropicta*—USNM 101960, lectotype (Dall, 1925:36), left valve; length, 39.9 mm; height, 34.3 mm; convexity, 9.6 mm [pair would be about 19.2 mm] (Figure 17). USNM 678001, paralectotype, right valve; ANSP 51749, possible paralectotype, right valve. Soquel [Capitola], Santa Cruz Co., California (36°53′N, 121°52′W), on beach; W. H. Dall.

S. ashleyi—LACM 4789, holotype, pair; length, 40.5 mm; height, 37.0 mm; convexity, 23.6 mm (not figured here). LACM Loc. 305C, "exposure at base of hill, 100′W and 440′S of NE corner of Sec. 8, T.19S., R.2W, USGS topo. map, San Ysidro quad." (approx. 32°32′30″N, 117°6′W) (LACM 4790–4804, paratypes, LACM Locs. 305, 305C, 318); San Diego Formation; middle Pliocene.

Description: Medium-sized (length to 52.0 mm; MCZ 60100; Eagle Island, Puget Sound, Washington); oblong; equivalve; shells average in thickness; much longer, rounded anteriorly; slightly truncate posteriorly; antero-dorsal margin concave near beaks, with a long lunule, rounded anteriorly; postero-dorsal margin rounded, lacking an escutcheon. Periostracum thin, tan to olive. Sculpture of fine concentric ribs in some; heavy, irregular concentric ribs in other material, particularly southern populations; fine radial sculpture also present. Externally white, with reddish rays; white internally. Pallial sinuses large.

I have illustrated a pair from British Columbia (CAS 064531) (Figure 18).

Distribution and habitat: Alaska: ?Seldovia Bay, Kenai Peninsula (59°28′N, 151°42′W) (LACM 73-18; two juvenile pairs, perhaps the result of unusual larval settlement); near Sitka, Baranof Island (57°3′N, 135°20′30″W) (Smith Coll., cited by Rae Baxter, in corresp., 13 June 1987); Yamani Cove, Baranof Island (56°40′20″N, 135°10′30″W) (Univ. Alaska Mus. M-759; N. Foster, in corresp., 9 and 27 July 1987); Craig, Prince of Wales Island, Alaska (55°27′N, 133°8′W) (LACM 17-3.1), south to Puget Sound, Washington (approx. 47°30′N, 123°W) (USNM 130631, 184279, and many other lots in various institutions). Not yet reported from the outer coast of Washington or Oregon. Van Damme Beach State Park, Mendocino Co., California (39°18′N, 113°48′W) (LACM 64-8), to Isla Asunción, Pacific coast of Baja California Sur (27°6′N, 114°17′W) (LACM 67-66). In the Gulf of California: near Bahía Willard, Baja California Norte (29°52′30″N, 114°23′30″W) (LACM 69-23), and possibly at Guaymas, Sonora (27°55′N, 110°53′W) (SDNHM 15261). Intertidal zone to 55 m (mean, 19 m), in sandy rubble. I have examined 182 lots.

This species has been recorded from late Pleistocene strata from Cayucos, San Luis Obispo Co., California

(VALENTINE, 1958:690), to Bahía Magdalena, Baja California Sur (JORDAN, 1936:112), with many intermediate records by various authors; in early Pleistocene deposits in the San Pedro area (for example, T. OLDROYD, 1925: 7; CLARK, 1931:opp. p. 30), and in the Pliocene of California (for example, WOODRING *et al.*, 1941:33, opp. p. 78; pl. 11, fig. 18; WOODRING & BRAMLETTE, 1951:88; pl. 14, fig. 12; ADEGOKE, 1969:125).

Discussion: *Semele ashleyi* Hertlein & Grant, from the middle Pliocene San Diego Formation, was differentiated from *S. rubropicta* by its (1) coarser concentric sculpture, separated by wider, more incised grooves, and (2) less developed lunule. These features are within the range of variability of this species. The average specimens of *S. rubropicta* from southern California and northern Baja California have still coarser sculpture than the type material of *S. ashleyi*. The lunule is indeed minimal on the type material of *S. ashleyi*, but it can be obscure in some Recent specimens as well.

A closely related species is *Semele fausta* Nomland (NOMLAND, 1917:233–236, 248; pl. 9, figs. 3, 3a, 3b) from the Pliocene upper Etchegoin Formation of Fresno Co., California. Its beaks are more pointed and closer to the posterior end, at least in the illustrated type specimen, than in any specimens I have seen of *S. rubropicta*.

Semele (*S.*) *solida* (Gray, 1828)

(Figures 19, 20)

Amphidesma solidum Gray, 1828: GRAY, 1828:6 [the figures cited, "pl. 6, figs. 6, 6a," never published] [as "*A. solida*"]; SOWERBY, 1833a:7; HANLEY, 1843:43; 6; pl. 12, fig. 32; 1856:341; REEVE, 1853:pl. 2, fig. 10; HUPÉ, in Gay, 1854:359; 1858:pl. 7, figs. 1–1c; HANLEY, 1857:pl. 2, fig. 4; PHILIPPI, 1860:175; TRYON, 1869:122 [*Semele*]; LAMY, 1908:52; DALL, 1909:160, 272, 280 [but not p. 294; pl. 28, fig. 10, which is *S. corrugata*]; LAMY, 1913: 360–361; DALL, 1915:25; SCHRÖDER, 1916:101–129; figs. 1–13; MARINCOVICH, 1973:14; fig. 21; OSORIO,1979: 32–33; fig. 38; BERNARD, 1983:47.

Amphidesma rugulosum Sowerby, in Darwin, 1846: SOWERBY, in Darwin, 1846:38.

Amphidesma orbicular Hupé, in Gay, 1854: HUPÉ, in Gay, 1854:359 [in synonymy with *A. solida*]; HUPÉ, in Gay, 1858:pl. 7, figs. 1–1c [as *A.* "*orbiculare*"; placed in synonymy by the earlier text].

Type material and locality: *A. solidum*—BM(NH) 1986084, **lectotype (here designated),** pair; length, 50.9 mm; height, 48.5 mm; convexity, 24.6 mm (Figure 19). This specimen is too small to match the length originally given (63.5 mm); it does not closely match the sketch on the unpublished MS plate in the BM(NH), so we must assume that there was more than one original specimen. Arica, Tarapaca Prov., "Peru" [Chile] (18°28′S, 70°20′W); W. Hennah.

A. rugulosum—BM(NH) 1987058, **lectotype (here designated),** right valve; length, 83.1 mm; height, 75.1 mm; convexity, 22.4 mm [pair would be 44.8 mm] (Figure 20). Bahía Herradura [de Guayacan], Coquimbo Prov., Chile (29°58′S, 71°22′W); marine terrace; [middle Pleistocene]; C. Darwin, 14–20 May 1835 (DARWIN, 1962: 343–346). BM(NH) 1837.12.1.3673, possible paralectotype, pair. Possibly from the second locality: Coquimbo, Coquimbo Prov., Chile (29°57′S, 71°21′W), on beach; C. Darwin, 14–20 May 1835.

Description: Large (Recent material to 80.8 mm; NRS UH Lam. 2283; Isla Quenu, Golfo de Ancud, Llanquihue Prov., Chile); rounded; right valve a little more inflated (decidedly more in a very few); shells heavy; longer anteriorly in most, rounded; slightly truncate posteriorly; antero-dorsal margin concave near beaks, with a lunule, convex anteriorly; postero-dorsal margin slightly convex, with a small escutcheon in left valve. Periostracum light olive to dark, present only as ventral shreds in adult. Sculpture of wavy concentric ribs, which are strong on posterior slope, and few obscure radial ribs. White exteriorly; internally generally white, sometimes with a yellowish tinge; hinge purple at ends; valve margins purple in some. Pallial sinuses large. Anterior lateral in right valve large, produced ventrally.

Distribution and habitat: Callao, Lima Prov., Peru (12°3′S, 77°10′W) (USNM 12550, 368501; LACM 35-6), to Pumalin, Golfo de Corcovado, Chiloe Prov., Chile (42°42′S, 72°52′W) (LACM 75-41). Depth records are from the intertidal zone to 11 m (mean, 3 m). The only habitat information available is that given by MARINCOVICH (1973:14): "buried in sand and gravel among boulders in lower intertidal zone." It is of minor commercial importance in Chile (OSORIO, 1979). I have seen 57 lots.

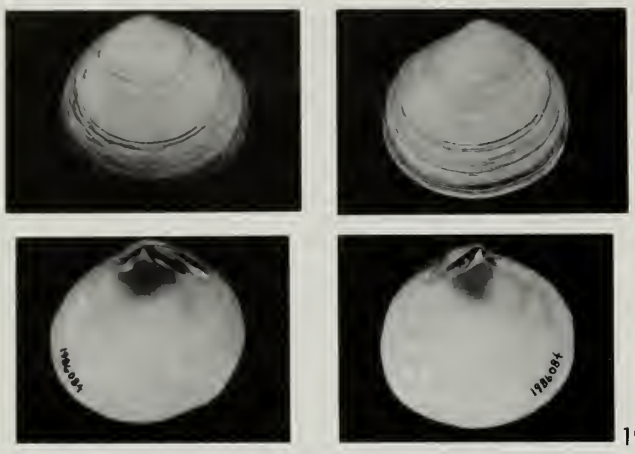
It has been reported from the Archipiélago de los Chonos, Chiloe Prov., Chile (about 45°S) (PHILIPPI, 1860:175; repeated by DALL, 1909:160, and by SOOT-RYEN, 1959: 64), but I have not seen any material to confirm this.

SOOT-RYEN's (1959:63) records of *Semele corrugata* (Sowerby) from 41°3′S to 41°50′S are based on specimens of *S. solida* (NRS).

The record of this species from the Galápagos Islands (PILSBRY & VANATTA, 1902:551) was based on a specimen of *Semele flavescens* (Gould) (CAS 064527).

RÜEGG (1957:830) reported this species from Pleistocene strata in Ica Prov., Peru. LAMY (1908:52) and JORDAN (1929:117–118) recorded it as a fossil at Coquimbo, Jordan calling the strata "Pliocene." HERM (1969:120–121; pl. 10, fig. 1) reported this species, as "*Semele corrugata*," from the upper and middle Pleistocene from several localities in Chile, including the deposit at Bahía Herradura, Coquimbo, which he regards as being of middle Pleistocene age.

Remarks: The Sowerby MS name, *Amphidesma rugulosum*, was introduced by DARWIN (1846), with a brief description by Sowerby, for fossil and Recent material from



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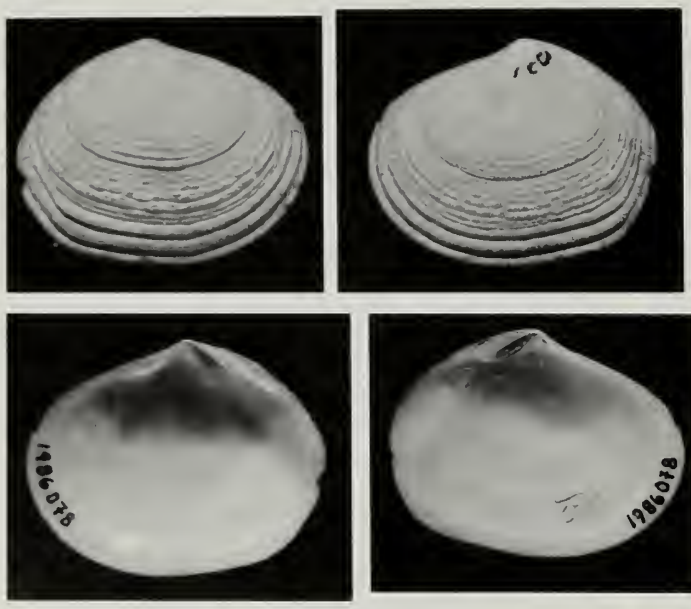

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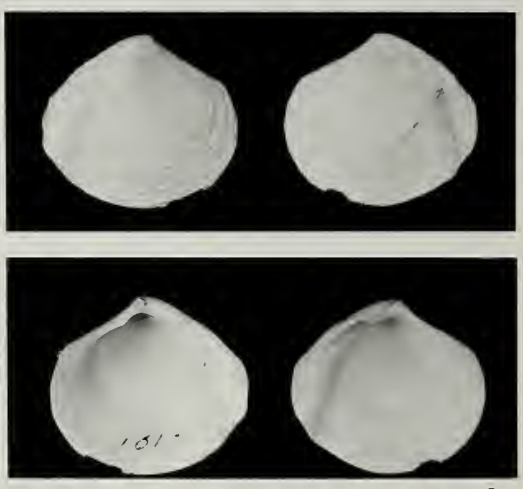

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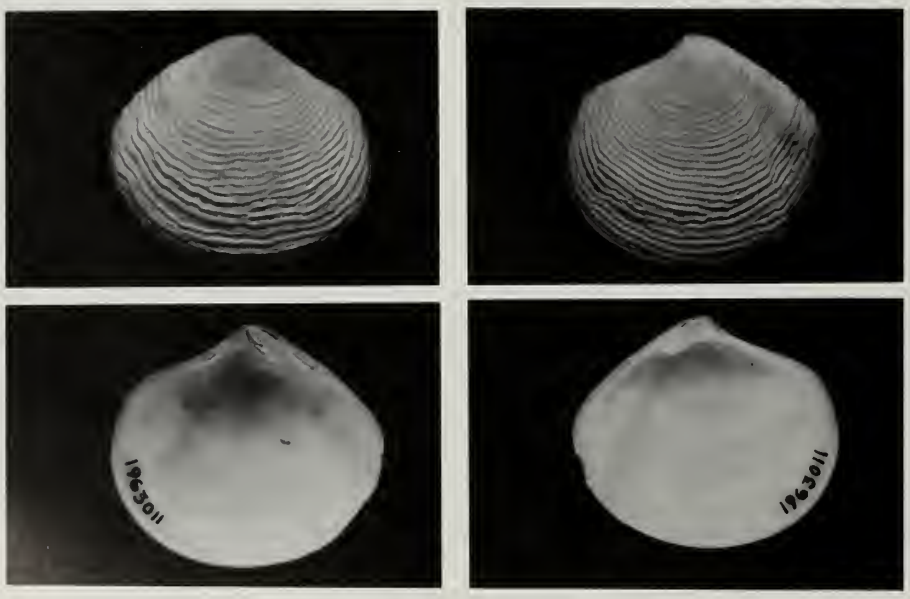

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near Coquimbo, Chile, where *Semele solida* is common and the only *Semele* present, so it could be nothing else. The brief statement comparing Recent and fossil specimens is sufficiently descriptive for the name to be taken as available. As far as I know, aside from reprints of DARWIN (1846), this name has not appeared elsewhere.

Semele solida is compared with the closely related *S. corrugata* under the latter. Previously published distributional information about these species is suspect because they have been much confused. In some collections, the concepts of the two were reversed.

Amphidesma croceum Gould, 1850, has been synonymized with this species by some authors (for example, DALL, 1909:280), but it belongs under *Semele corrugata*.

In spite of the fact that this species is uncommon in collections in the U.S., it is the best known *Semele* anatomically, owing to the detailed monograph of SCHRÖDER (1916).

Semele (*S.*) *sowerbyi* Tryon, 1869

(Figure 21)

Amphidesma punctatum Sowerby, 1833: SOWERBY, 1833a:8; pl. 18, fig. 7; SOWERBY, 1833b:200; HANLEY, 1843:45; 7; pl. 12, fig. 46; 1856:341; REEVE, 1853:pl. 4, fig. 26; CARPENTER, 1857b:182, 304; HANLEY, 1857:pl. 3, fig. 27; LAMY, 1913:355; 358, footnote; KEEN, 1958:198; OLSSON, 1961:360, 365, 537; pl. 64, fig. 2; KEEN, 1971: 253–254; fig. 642.

[*non Amphidesma punctatum* Say, 1822]: SAY, 1822:308 [as *A. punctata*].

Semele sowerbyi Tryon, 1869 [replacement name for *A. punctatum* Sowerby, *non* Say]: TRYON, 1869:122.

[*non S. sowerbyi* LAMY, 1912:165].

Semele clydosa Bernard, 1983 [unnecessary replacement for *A. punctatum* Sowerby, *non* Say]: BERNARD,1983:46, 69.

Amphidesma formosa Sowerby, *auctt., non* Sowerby, 1833: REEVE, 1841:68; pl. 48, fig. 7.

[*non* SOWERBY, 1833a:7, 8; pl. 19, fig. 8].

Semele decisa (Conrad), *auctt., non* Conrad, 1837: DALL, 1915: 25 [in part].

[*non* CONRAD, 1837:239; pl. 19, fig. 2].

Type material and locality: *A. punctatum* Sowerby—BM(NH) 1986078, **lectotype (here designated),** the figured syntype, pair; length, 43.9 mm; height, 34.0 mm; convexity, 14.3 mm (Figure 21). BM(NH) 1907.10.28.21, paralectotype. Galápagos Islands, Ecuador (about 0°30′S, 91°W); H. Cuming, 1828–1830.

Description: Medium-sized (to 59.6 mm; UCMP B.3615; Isla Santa Cruz, Galápagos); oblong; right valve slightly more inflated; average in thickness; longer, rounded anteriorly; rounded posteriorly; antero-dorsal margin straight, with a small lunule; postero-dorsal margin slightly rounded, lacking an escutcheon, with a slight flexure to the right. Periostracum thin, tan. Sculpture of heavy concentric ribs that are punctate on the young part of shell; also with finer concentric riblets overriding heavy concentric ribs on the mature part of shell. White externally, with reddish radial rays and small reddish flecks along dorsal margin; white to deep yellow within; hinge slightly purple. Pallial sinuses large.

Distribution and habitat: Restricted to the Galápagos Islands: Fernandina (CAS 064529), Isabela (CAS 064528, 064530), Rábida (LACM 71-69), and Santa Cruz (SBMNH 34899, USNM 752921, LACM 66-121, UCMP B.3615, Skoglund Coll.) (approx. 0°15′–1°S, 90°15′–91°45′W). Intertidal zone to 13 m (mean, 6 m); the only bottom type recorded is sand. I have examined 10 lots.

This species has been reported from strata of late Pleistocene age on Isla San Salvador in the Galápagos (HERTLEIN & STRONG, 1939:369).

Remarks: As has been mentioned by other authors, this species is closest to the Californian *Semele decisa* (Conrad), from which it differs in being smaller, more elongate, and more punctate.

Semele (*S.*) *tortuosa* (C. B. Adams, 1852)

(Figures 22, 23)

Amphidesma tortuosum C. B. Adams, 1852: C. B. ADAMS, 1852a:515, 547 [1852b:291, 323]; CARPENTER, 1857b: 280, 303 [*Semele*]; CARPENTER, 1864a:367 [1872:203]; TRYON, 1869:122; LAMY, 1913:331, footnote; TURNER, 1956:92–93, 126–127; pl. 17, figs. 10, 11; KEEN, 1958: 200–201; fig. 501; OLSSON, 1961:360, 365, 537; pl. 64, figs. 3–3b; KEEN, 1971:255–256; fig. 650; TAYLOR *et al.*, 1973:266; pl. 5, figs. 1, 2, 4; table 10; BERNARD, 1983: 47.

Semele planata Carpenter, 1856: CARPENTER, 1856:160; CARPENTER, 1857b:284, 303; TRYON, 1869:121; LAMY, 1913:331, footnote; KEEN, 1958:198; PALMER, 1963:314, 394; pl. 64, figs. 6–9; KEEN, 1971:255 [as a synonym of *S. tortuosa*].

Type material and localities: *A. tortuosum*—MCZ 186366, holotype, pair; length, 30.6 mm; height, 27.3 mm; convexity, 8.0 mm (Figure 22). Panama, presumably near Panama City (about 8°58′N, 79°32′W); C. B. Adams, 27 Nov. 1850–2 Jan. 1851.

S. planata—BM(NH) 1986078, holotype, pair; length, 39.9 mm; height, 35.0 mm; convexity, 11.6 mm (Figure 23). Panama Bay; T. Bridges, spring 1856.

←

Explanation of Figures 19 to 23

Figures 19 and 20. *Semele* (*S.*) *solida* (Gray). Figure 19: **Lectotype** (herein) of *Amphidesma solidum*; length, 50.9 mm. Figure 20: **Lectotype** (herein) of *A. rugulosum* Sowerby; length, 83.1 mm.

Figure 21. *Semele* (*S.*) *sowerbyi* Tryon. **Lectotype** (herein) of *Amphidesma punctatum* Sowerby (*non* Say); length, 43.9 mm.

Figures 22 and 23. *Semele* (*S.*) *tortuosa* (C. B. Adams). Figure 22: Holotype of *Amphidesma tortuosum*; length, 30.6 mm. Figure 23: Holotype of *S. planata* Carpenter; length, 39.9 mm.

Description: Medium-sized (length to 56.2 mm; McClincy Coll.; Bahía San Carlos, Sonora, Mexico); rounded; not as convex as other species; right valve more inflated; shells average in thickness; longer, produced, rounded anteriorly; truncate and conspicuously flexed posteriorly, right valve with a pronounced, broad radial rib at edge of posterior slope, left valve with a corresponding conspicuous furrow; antero-dorsal margin relatively straight to slightly concave, with a broad, elongate lunule; postero-dorsal margin straight, with a broad escutcheon. Periostracum thin, tan. Sculpture of well-spaced, heavy, wavy, concentric ribs. White externally, with reddish flecks along dorsal margin; white to orange-yellow within; hinge with a purple stain at anterior end of beaks. Pallial sinuses medium in size.

The shell structure of this uncommon species was discussed by TAYLOR *et al.* (1973).

Distribution and habitat: Bahía San Carlos, Sonora, Mexico (27°56′N, 111°4′W) (CAS 064716; SBMNH 34898), to Puerto Palmar, Guayas Prov., Ecuador (2°2′S, 80°44′W) (OLSSON, 1961). I have not seen specimens from further south than Panama Bay, but there is little reason to doubt Olsson's record. Records are from the intertidal zone to 55 m (mean, 21 m), on sand and rocky substrates. It is uncommon; I have examined only 17 lots.

(*Amphidesma*) Lamarck, 1818

(*Amphidesma*) LAMARCK, 1818:489–493.
Type species: *A. variegata* LAMARCK, 1818:490; by subsequent designation of CHILDREN, 1823:300–301; =*Tellina purpurascens* GMELIN, 1791:3288; western Atlantic and eastern Pacific.

Like the preceding subgenus, *Semele, s.s.,* this may be polyphyletic, but it is used here to provide a convenient grouping for some eastern Pacific species. In general, these species are thinner-shelled than *Semele,* more elongate, and tend to have discrepant sculpture (that is, the sculpture in the two valves differs). In general, they occur farther offshore than species of *Semele* and more often on soft bottoms, mud, or sand.

This subgenus was occasionally incorrectly used in the Mesodesmatidae.

Semele (*A.*) *craneana* Hertlein & Strong, 1949

(Figures 24, 25)

Semele craneana Hertlein & Strong, 1949: HERTLEIN & STRONG, 1949:240–242, 258; pl. 1, figs. 19, 22; KEEN, 1958:196–197; fig. 479; OLSSON, 1961:360, 539; pl. 66, fig. 2 [not in main text]; KEEN, 1971:249–250; fig. 628; BERNARD, 1983:46.

Type material and locality: CAS 064521 (*ex* CASGTC 9249), holotype, left valve; length, 37.9 mm; height, 29.0 mm; convexity, 6.2 mm [pair would be about 12.4 mm] (Figure 24). Southern Gulf of California; exact locality unknown; **type locality here restricted to Arena Bank, Baja California Sur** (23°27′N, 109°24′W), where HERTLEIN & STRONG (1949) reported the species from two stations, yielding specimens that are regarded as paratypes: CAS 064497 (*ex* SUPTC 8056), from Loc. 136-D-24; CAS 064534 (*ex* CAS 17714) (Figure 25) and AMNH 160337 from Loc. 136-D-26.

Description: Medium-sized (length to 42.0 mm; Skoglund Coll.; N of Isla Danzante, Baja California Sur); oblong; equivalve; shells thin to average in thickness; longer, sharply rounded anteriorly; decidedly truncate posteriorly; antero-dorsal margin almost straight, with a narrow lunule; postero-dorsal margin straight, with an indistinct escutcheon. Periostracum light tan. Sculpture of heavy, rounded concentric ribs, some of which are oblique near posterior end. White to yellowish externally, rayed and blotched with red, purple, and/or tan; these colors showing through into interior. Pallial sinuses large.

Distribution and habitat: Baja California Norte: Roca Consag (31°7′N, 114°29′W) (LACM 37-122). Baja California Sur: N of Isla Danzante (Skoglund Coll.); NW end of Isla Smith (Skoglund Coll.); Arena Bank (see **Type material**), Isla Cerralvo (MCZ 253664), Los Frailes (Skoglund Coll.), and 5.6 km off Roca Piramide, Isla Clarion, Islas Revillagigedos (18°19′N, 114°45′W) (CAS 064533). Sonora: Punta San Antonio (27°57′N, 111°7′W) (Skoglund Coll.). Depth records are from 32 to 110 m (mean, 78 m), on mud and sand substrates. I know of only 11 lots.

Remarks: HERTLEIN & STRONG (1949) compared their new species to two taxa unrelated to it—the eastern Pacific *Semele tabogensis* Pilsbry & Lowe, here regarded as a synonym of *S. rosea* (Sowerby), and the western Atlantic *S. martini* (Reeve, 1853), regarded as a synonym of the African *S. modesta* (Reeve, 1853) by BOSS (1972:13–14). The closest ally is probably *S.* (*A.*) *purpurascens* (Gmelin), which is discussed below and differs in lacking heavy concentric ribs as an adult. Juvenile *S. craneana,* however, are smooth and not unlike *S. purpurascens,* differing in being flatter.

Semele (*A.*) *formosa* (Sowerby, 1833)

(Figures 26–28)

Amphidesma formosum Sowerby, 1833: SOWERBY, 1833a:7, 8; pl. 19, fig. 8; SOWERBY, 1833b:199; HANLEY, 1843: 44; 7; pl. 12, fig. 48; 1856:341; REEVE, 1853:pl. 4, fig. 27; HANLEY, 1857:pl. 3, fig. 25; TRYON, 1869:120 [*Sem-*

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Explanation of Figures 24 to 28

Figures 24 and 25. *Semele* (*Amphidesma*) *craneana* Hertlein & Strong. Figure 24: Holotype of *S. craneana*; length, 37.9 mm. Figure 25: CAS 064534; paratype of *S. craneana*; length, 26.0 mm.

Figures 26–28. *Semele* (*A.*) *formosa* (Sowerby). Figure 26: Lectotype of *Amphidesma formosum*; length, 50.6 mm. Figure 27: Holotype of *S. verruculastra* Keen; length, 42.6 mm. Figure 28: LACM 72-63; Isla del Caño, Costa Rica; length, 55.3 mm.

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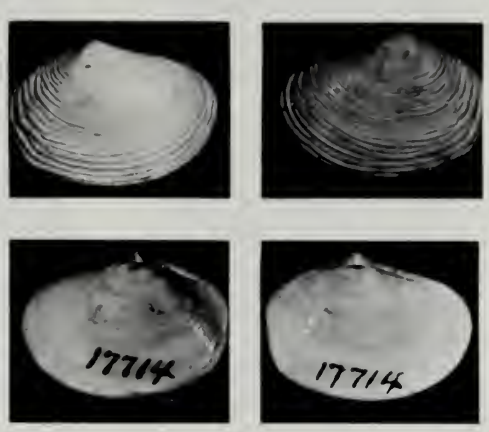

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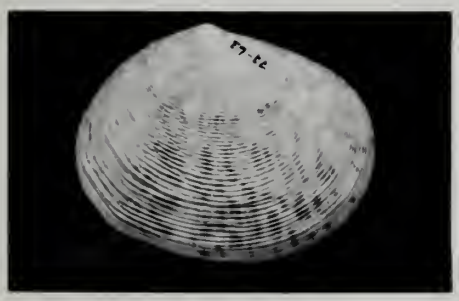

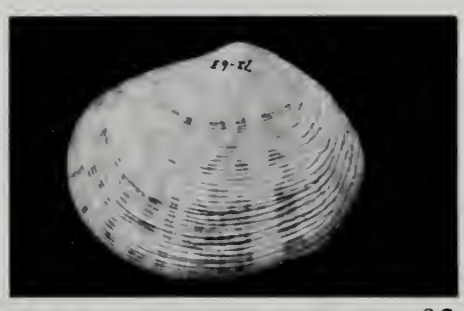

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ele]; VERRILL, 1870:218–219; DALL, 1909:271; LAMY, 1913:355; DALL, 1915:26; HERTLEIN & STRONG, 1949: 240, 249; KEEN, 1958:196–197; fig. 482; OLSSON, 1961: 360, 365, 558; pl. 85, fig. 8; KEEN, 1971:251–252; fig. 631; COAN, 1983:133–134; figs. 1, 2; BERNARD, 1983: 46.

[but not REEVE, 1841:68; pl. 48, fig. 7; =*A. punctata* Sowerby].

Semele verrucosa Mörch, *auctt.*, *non* Mörch, 1860: HERTLEIN & STRONG, 1949:240, 249, 258; pl. 1, figs. 21, 24; KEEN, 1958:202–203; fig. 504; OLSSON, 1961:360, 366, 538; pl. 65, figs. 1–1b; EMERSON & HERTLEIN, 1964:356, 357; 359–360; figs. 3i, j.

[*non* Mörch, 1860:190–191].

Semele verruculastra Keen, 1966: KEEN, 1966b:32–33; KEEN, 1971:255–257; fig. 653; COAN, 1983:133–134 [as a synonym of *S. formosa*]; BERNARD, 1983:47.

Type material and localities: *A. formosum*—BM(NH) 1907.10.28.20, lectotype (COAN, 1983:133), right valve, the specimen in Sowerby's uppermost figure; length, 50.6 mm; height, 40.9 mm; convexity, 9.8 mm [pair would be about 19.6 mm] (Figure 26). Bahía Santa Elena, Guayas Prov., Ecuador (2°12′S, 80°52′W), 13 m; H. Cuming, 1828–1830. (The pair figured by Olsson, 1961, as "holotype" could not have been from the original lot because "only two odd valves" were originally collected.)

S. verruculastra—CAS 036679 [*ex* CASGTC 9256], holotype, right valve; length, 42.6 mm; height, 32.5 mm; convexity, 6.5 mm [pair would be about 13.0 mm] (Figure 27). Hannibal Bank, Panama (7°23′30″N, 80°3′W), about 68 m; CAS Loc. 17996.

Description: Medium-sized (length to 77.0 mm; Kerstitch Coll.; Bahía Bocochibampo, Sonora, Mexico); oblong; equivalve; average in thickness; longer, rounded anteriorly; somewhat truncate, flexed to the left posteriorly; antero-dorsal margin fairly straight, with a narrow elongate lunule; postero-dorsal margin slightly rounded, without an escutcheon. Periostracum not evident. Sculpture of regular concentric ribs that are frilly at anterior and posterior ends of valves, and broken into alternating imbrications near center of right valve and in dorsal area of left valve; fine radial striae present. Externally with radial brown lines that are generally broken into patches; beaks with a V-shaped white patch; white to yellow-orange within, with the external brown patches showing through; hinge purple. Pallial sinuses large.

Because the type specimens are both right valves, I have illustrated a pair from Costa Rica (LACM 72-63) (Figure 28).

Distribution and habitat: Isla San Pedro Mártir (28°22′N, 112°21′W) (CAS 064889) and Bahía San Carlos, Sonora (27°56′N, 111°4′W) (SBMNH 34913; Skoglund Coll.), and Isla San Marcos, Baja California Sur (27°12′N, 112°5′W) (CAS 064535; UCMP R.7103), Mexico, to Bahía Santa Elena, Guayas Prov., Ecuador (2°12′S, 80°52′W) (type loc.); Isla del Coco, Costa Rica (CAS 051865). I have not seen any specimens other than the type material from further south than the Archipiélago de las Perlas, Panama (Skoglund Coll.; and OLSSON, 1961, as "*S. verrucosa*"), but there is little reason to doubt the type locality. Depth records are from 1.5 to 68 m (mean, 22 m), on sand. I have examined 32 lots.

A record from Puertecitos (DUSHANE, 1962:49), further north in the Gulf of California, cannot be verified and was probably based on a misidentification.

HOFFSTETTER (1948:80) reported this species, with some doubt, from Pleistocene strata on Ecuador's Santa Elena Peninsula.

Semele (*A.*) *pallida* (Sowerby, 1833)

(Figures 29–31)

Amphidesma pallidum Sowerby, 1833: SOWERBY, 1833a:7, 8; pl. 17, fig. 3; SOWERBY, 1833b:199; REEVE, 1841:67; pl. 47, fig. 3; HANLEY, 1843:44; 7; pl. 12, fig. 44; 1856:341; REEVE, 1853:pl. 4, fig. 22; HANLEY, 1857:pl. 3, fig. 32; TRYON, 1869:121 [*Semele*]; DALL, 1909:272; LAMY, 1913: 354, footnote; OLSSON, 1961:360, 364, 539; pl. 66, fig. 8; KEEN, 1971:253–254; fig. 638; BERNARD, 1983:47.

Semele regularis Dall, 1915, *non* Smith, 1885: DALL, 1915: 27.

[*non* SMITH, 1885:87; pl. 5, figs. 4–4b, an Australian *Abra*].

Semele simplicissima Pilsbry & Lowe, 1932: PILSBRY & LOWE, 1932:93, 144; pl. 12, figs. 6, 6a; HERTLEIN & STRONG, 1949:240, 247; KEEN, 1958:200–201; fig. 497; OLSSON, 1961:364 [as a synonym of *S. pallida*]; KEEN, 1971:254–255; fig. 647; BERNARD, 1983:47; HERTZ, 1986:41.

Semele paziana Hertlein & Strong, 1949 [new name for *S. regularis* Dall, *non* Smith]: HERTLEIN & STRONG, 1949: 240; 247, incl. footnote; KEEN, 1958:198–199; fig. 490; OLSSON, 1961:364 [as a synonym of *S. pallida*]; PARKER, 1964a:161; pl. 5, fig. 22; PARKER, 1964b:pl. 5, fig. 22; KEEN, 1971:253–254; fig. 639; BERNARD, 1983:47.

Type material and localities: *A. pallidum*—BM(NH) 1986077/1, **lectotype (here designated),** the figured syntype, pair; length, 30.6 mm; height, 22.8 mm; convexity, 11.8 mm (Figure 29). BM(NH) 1986077/1, 2, paralectotypes. [Isla] Salango, Manabi Prov., Ecuador (1°35′S, 80°52′W), 13 m, sandy mud; H. Cuming, 1828–1830.

S. regularis Dall/*S. paziana*—USNM 96433, **lectotype (here designated),** right valve; length, 21.0 mm; height, 16.0 mm; convexity, 3.6 mm (Figure 30). USNM 859082, paralectotype, 1 valve. Off La Paz, Baja California Sur,

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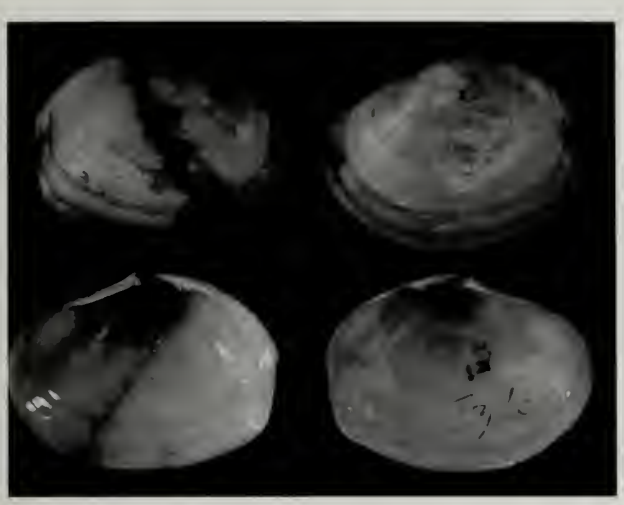
Explanation of Figures 29 to 34

Figures 29–31. *Semele* (*A.*) *pallida* (Sowerby). Figure 29: **Lectotype** (herein) of *Amphidesma pallidum*; length, 30.6 mm. Figure 30: **Lectotype** (herein) of *S. regularis* Dall (*non* Smith); length, 21.0 mm. Figure 31: Holotype of *S. simplicissima* Pilsbry & Lowe; length, 19.9 mm.

Figures 32–34. *Semele* (*A.*) *purpurascens* (Gmelin). Figure 32: Type figure from LISTER (1687); length, 32 mm. Figure 33: **Lectotype** (herein) of *S. sparsilineata* Dall; length, 14.6 mm. Figure 34: LACM 34-146; Bahía Tenacatita, Jalisco, Mexico; length, 20.9 mm.



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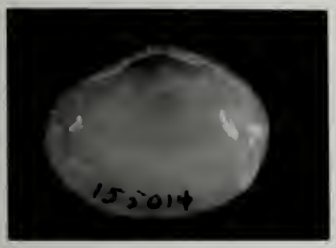

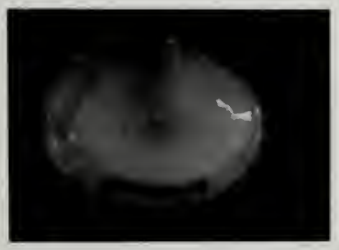

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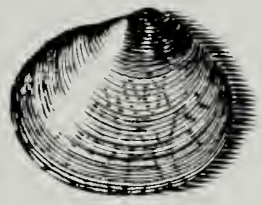
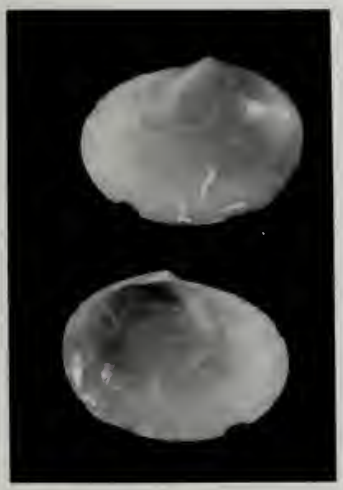


144. pedunculus tenuis, ex violo purpurascens, radiatus.

32



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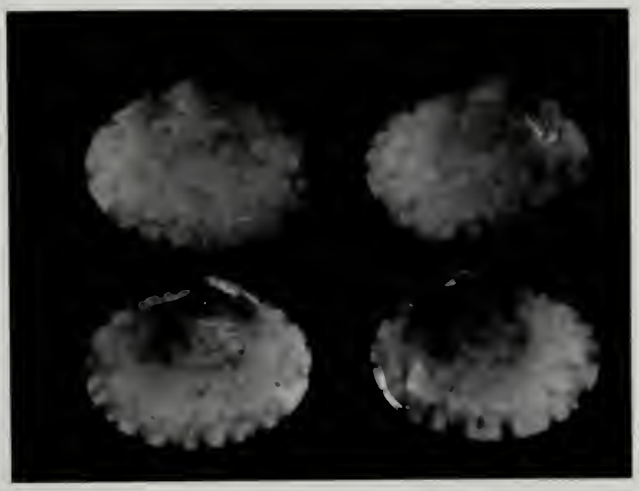

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Mexico, *Albatross* stn. 2823 (24°18′N, 110°22′W), sand [label] or broken shell [log], 48 m; 30 April 1888.

S. simplicissima—ANSP 155014, holotype, pair; length, 19.9 mm; height, 14.8 mm; convexity, 7.6 mm (Figure 31). Acapulco, Guerrero, Mexico (16°51′N, 99°56′W), 37 m; H. N. Lowe, April 1930.

Description: Medium-sized (length to 41.1 mm; SBMNH 34914; Empalme, Sonora, Mexico); oblong; equivalve; thin-shelled; longer, sharply rounded anteriorly; truncate posteriorly; antero-dorsal margin concave near beaks, with a lunule, straight to convex anteriorly; postero-dorsal margin slightly convex, with an escutcheon. Periostracum with an iridescent sheen, present only as ventral shreds in many adult specimens. Sculpture of fine, closely spaced concentric ribs that are half as numerous on posterior slope. White externally and internally, but often with pink or orange hue near beaks and internally. Pallial sinuses medium in size.

Distribution and habitat: Gulf of California as far north as Bahía San Carlos, Sonora (27°56′N, 111°4′W) (CAS 064542, 064543), and Bahía Concepción, Baja California Sur (25°10′N, 111°55′W) (CAS 064544), to Tumbez, Tumbez Prov., Peru (3°31′S, 80°25′W) (LACM 72-83). From 13 to 128 m (mean, 45 m), on sand and mud. I have examined 62 lots.

Discussion: Olsson (1961) was correct in synonymizing *Semele paziana* and *S. simplicissima* with *S. pallida.* Dall (1915) did not compare his *S. regularis* (*non* Smith; later renamed *S. paziana*) with *S. pallida,* nor did Pilsbry & Lowe (1932) compare their *S. simplicissima* with *S. pallida.* The supposed distinction in the presence or absence of concentric striae between concentric ribs that some authors have advanced proves not to be useful.

Semele (*A.*) *purpurascens* (Gmelin, 1791)

(Figures 32–34)

Venus purpurascens Gmelin, 1791: Gmelin, 1791:3288 [spelled *V.* "*pupurascens,*" in Rudolphipoli printing]; Dall, 1900:993 [*Semele*]; Lamy, 1913:350–353; Boss, 1972:7, 13, 15–20, 24; pl. 3; pl. 5, fig. D; pl. 6, figs. A–D; pl. 7, fig. E; pl. 8, fig. D; pl. 10, fig. C.

Tellina obliqua Wood, 1815: Wood, 1815:152; pl. 41, figs. 4, 5 [name suppressed, ICZN Opinion 948, 29 March 1971]; Carpenter, 1857b:284, 303 [*Semele*].

Amphidesma variegata Lamarck, 1818: Lamarck, 1818:490 [based, in part, on Lamarck, 1798:pl. 291, fig. 3]; Hupé, in Gay, 1854:359–360; 1858:pl. 7, fig. 2; Dall, 1909: 272 [*Semele*]; Lamy, 1913:353.

Semele sparsilineata Dall, 1915: Dall, 1915:26; Hertlein & Strong, 1949:240, 247–248, 258; pl. 1, fig. 8; Keen, 1958:200–201; fig. 498; Olsson, 1961:359, 363, 539; pl. 66, fig. 7; Cauquoin, 1969:577; Keen, 1971:255–256; fig. 649.

[Not to be confused with *Amphidesma purpurascens* Sowerby, 1833 (renamed *Semele sowerbyi* Tryon, 1869), see above; nor with *A. purpurascens* Lamarck, 1818:493, a synonym of *Ervilia nitens* (Montagu, 1808), according to Lamy (1912:165; 1913:328–329).]

Type material and localities: I have not searched for the type material of two of the three non-eastern Pacific synonyms.

V. purpurascens—One of Lister's figures (1687:pl. 303, fig. 144), one of three illustrations cited by Gmelin, was designated as the type figure by Boss (1972:17); length, 33 mm; height, 27.8 mm (Figure 32). Lister's collection is supposedly at Cambridge University, but none of his material has yet been recognized there (Dance, 1986:217). Boss (1972:15) designated Key West, Florida, as the type locality.

T. obliqua—Not searched. Boss (1972:16) also designated Key West, Florida, as the type locality of this synonym.

A. variegata—Muséum d'Histoire Naturelle, Geneva 1082/74/1, 2, syntypes, pairs; no. 1 is 43 mm in length; no. 2 is 40 mm in length. Although Lamarck indicated the origin of his material as "les côtes d'Afrique," the large pallial sinuses on these specimens suggest that they came from the western Atlantic, fortunate because Boss (1972: 16) designated Key West, Florida, as the type locality of this synonym. (The closely related west African species, *Semele lamyi* Nicklès, 1955, has conspicuously smaller pallial sinuses.)

S. sparsilineata—USNM 96269, **lectotype (here designated),** left valve; length, 14.6 mm; height, 11.0 mm; convexity, 3.6 mm [pair would be about 7.2 mm] (Figure 32). USNM 859083, paralectotypes, 4 valves. Panama Bay, Panama, *Albatross* stn. 2798 (8°10′30″N, 78°50′30″W), 33 m, sand; 5 March 1888.

Description: Small (length to 33.5 mm; ANSP 308233; Isla Taboga, Panama); oblong; equivalve; shells thin; longer, rounded anteriorly; somewhat truncate posteriorly; antero-dorsal margin straight, with a narrow lunule; postero-dorsal margin straight, with an indistinct escutcheon in left valve. Periostracum thin, tan. Sculpture of fine concentric threads that are especially oblique in left valve, running ventrally toward posterior end. Color white to orange externally and internally, with purple suffusion in many and brown flecks and rays; brown patterns generally showing through into interior. Pallial sinuses large.

I am illustrating an eastern Pacific pair from central Mexico in better condition than the type of *Semele sparsilineata* (LACM 34-146) (Figure 34).

The animal was figured by Hupé, in Gay (1858:pl. 7; fig. 2b), and the anatomy was discussed by Boss (1972:4–7; pl. 3).

Distribution and habitat: Gulf of California at Bahía San Carlos, Sonora (27°56′N, 111°5′W) (LACM 64-36), but with no specimens from elsewhere in the Gulf of California, south to Punta Ancon, Guayas Prov., Ecuador (2°20′S, 80°54′W) (SBMNH 34916); Isla del Coco, Costa

Rica (SBMNH 34915, 34940); Isla Isabela, Galápagos Islands, Ecuador (LACM 66-211). HUPÉ (in Gay, 1854) reported it from Peru and Chile. A Peruvian occurrence is plausible in that Hupé figured an animal. GIGOUX (1935: 284) also reported this species from Chile in Atacama Prov. There are no specimens in collections I have studied from either Peru or Chile. Records in the eastern Pacific are from the intertidal zone to 78 m (mean, 19 m), on rubble substrates. I have seen 56 eastern Pacific lots.

In the western Atlantic, BOSS (1972) reports it from Cape Fear, North Carolina, to Río de la Plata, Uruguay, from "shallow water" to 640 m on sand bottoms. It also occurs in formations of Miocene, Pliocene, and Pleistocene ages in the western Atlantic region. This species appears to be more common in the western Atlantic than it is in the eastern Pacific.

Discussion: The distinctions that workers have cited between *Semele purpurascens* from the western Atlantic and *S. sparsilineata* from the eastern Pacific are the latter's less-pronounced oblique grooving (DALL, 1915) and the belief that it is smaller, heavier, and less convex (OLSSON, 1961). However, the extent of grooving is variable (see BOSS, 1972:pl. 6, figs. A–D). The largest eastern Pacific specimen I have seen is 33.5 mm in length, only 2.5 mm less than the largest specimen that Boss cites from the western Atlantic, 36 mm. I measured five adult specimens from Key West, Florida (CAS 064545), and found a convexity-length ratio of 0.38 (±0.03) and a convexity-height ratio of 0.47 (±0.03). Five specimens of similar size from Esmeraldas, Ecuador (SBMNH 34901), had a convexity-length ratio of 0.41 (±0.02) and a convexity-height ratio of 0.49 (±0.02). Thus, some eastern Pacific material is as convex, if not more convex, than western Atlantic material. I have also found that shell thickness varies a great deal, perhaps depending on environmental conditions.

The name *Semele lamyi* Nicklès, 1955 (NICKLÈS, 1955: 202–204; fig. 32), was proposed for west African material based on differences in the pallial line, cardinal teeth, color, and sculpture. The last three characters are suspect, being variable in western Atlantic and eastern Pacific material of *S. purpurascens,* but the pallial sinus of the specimen figured by Nicklès is conspicuously smaller than any specimen I have seen of *S. purpurascens.*

Semele (*A.*) *venusta* (Reeve, 1853, *ex* A. Adams MS)

(Figures 35–37)

Amphidesma venustum Reeve, 1853, *ex* A. Adams MS: REEVE, 1853:pl. 1, fig. 3 [as "A. Adams"]; A. ADAMS, 1854:96 [*Semele*]; CARPENTER, 1857b:245, 303; 1864b:537, 668 [1872:23, 154]; TRYON, 1869:122; LAMY, 1913:356; DALL, 1915:27; HERTLEIN & STRONG, 1949:240, 248–249, 258; pl. 1, fig. 13; KEEN, 1958:200, 202–203; fig. 503; OLSSON, 1961:360, 370, 539; pl. 66, figs. 1, 1a; CAUQUOIN, 1969:577; KEEN, 1971:255–256; fig. 651; BERNARD, 1983:47.

Semele incongrua Carpenter, 1864: CARPENTER, 1864b:611, 640 [1872:97, 126]; CARPENTER, 1865:208–1866:209 [as *S.* "*incungrua*"]; TRYON, 1869:120; LAMY, 1913:354, footnote; DALL, 1915:27; I. OLDROYD, 1925:181; pl. 11, figs. 12, 13; GRANT & GALE, 1931:377; BURCH, 1945a: 18; 1945b:17; HERTLEIN & STRONG, 1949:240, 249; PALMER, 1958:16, 27, 38, 48, 110–111, 339; pl. 14, figs. 7–10; COAN, 1973:320–322; figs. 6, 7, 17; BERNARD, 1983:46.

Semele pulchra "var." *montereyi* Arnold, 1903: ARNOLD, 1903: 166–167, 392; pl. 15, figs. 3, 3a [not 4, 4a, as stated in text and in pl. expl.]; DALL, 1915:27 [as a synonym of *S. incongrua*]; GRANT & GALE, 1931:377; BURCH, 1945a: 18; HERTLEIN & STRONG, 1949:249 [as a subspecies of *S. incongrua*].

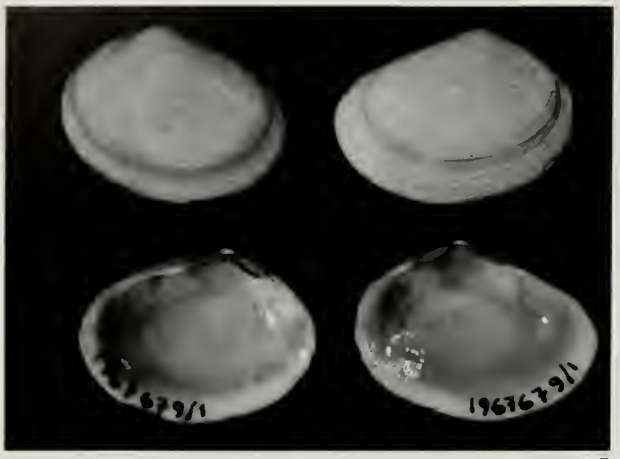
Type material and localities: *A. venustum*—BM(NH) 1967679/1, **lectotope (here designated),** the figured specimen, pair; length, 29.0 mm; height, 21.6 mm; convexity, 11.1 mm (Figure 35). BM(NH) 1967679/2, paralectotype. "West Colombia" [probably Ecuador]; H. Cuming, 1828–1830. **I here restrict the type locality to Manta, Manabi Prov., Ecuador** (0°57′N, 80°44′W), from where OLSSON (1961) reported the species.

S. incongrua—USNM 663888, lectotype (COAN, 1973: 320), pair; length, 14.1 mm; height, 10.0 mm; convexity, 4.7 mm (Figure 36). Catalina Island, Los Angeles Co., California (about 33°26′N, 118°29′W); 73–110 m; J. G. Cooper, 20–26 June 1863.

S. pulchra montereyi—USNM 162526, holotype, right valve; length, 18.7 mm; height, 15.0 mm; convexity, 3.8 mm [pair would be about 7.6 mm] (Figure 37). Deadman Island, San Pedro, Los Angeles Co., California (33°13′N, 118°1′W); lower San Pedro Formation, early Pleistocene; R. Arnold. (This island is no longer present in Los Angeles Harbor.)

Description: Small (length to 27.8 mm; LACM 39-97; Santa Rosa Island, California); ovate–ellipsoid; equivalve; shells thin; much longer, obliquely rounded anteriorly; rounded posteriorly; antero-dorsal margin slightly concave near beaks, with a lunule, convex anteriorly; postero-dorsal margin slightly convex, with an indistinct escutcheon in left valve. Periostracum not evident. Sculpture of concentric ribs, those in left valve smooth and rounded, except on posterior slope, those in right valve sharper, more lamellar, often scaly on posterior slope. Fine radial sculpture generally present between concentric ribs in both valves. Externally white, rayed with brown or purple, often with a lighter radial band in center of umbones, with flecks of purple on dorsal margin; internally purple or rose. Pallial sinuses very large.

Distribution: Monterey, Monterey Co., California (36°38′45″N, 121°56′W) (USNM 20438, 56330, 194332, 194335; LACM 124470, 38-157; UCMP E.8331; CAS 064554, 064557), into the Gulf of California as far north as Isla Smith (about 29°3′N, 113°13′W) (CAS 064546) and Isla Angel de la Guarda (about 29°3′N, 113°30′W)



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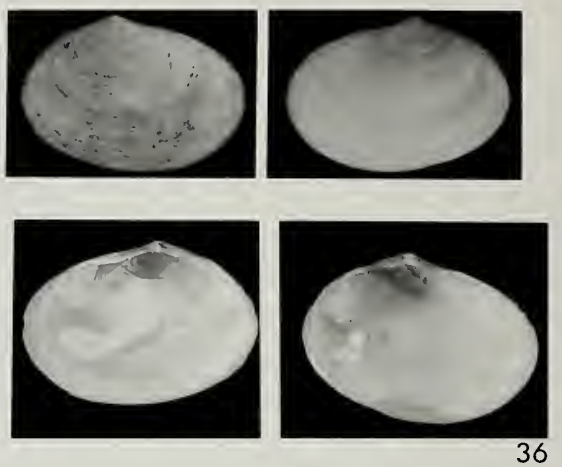

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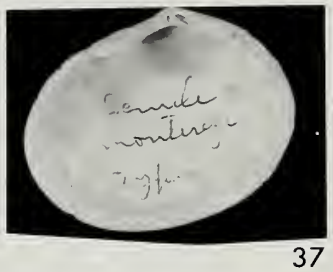

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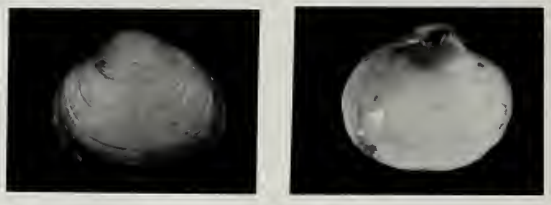

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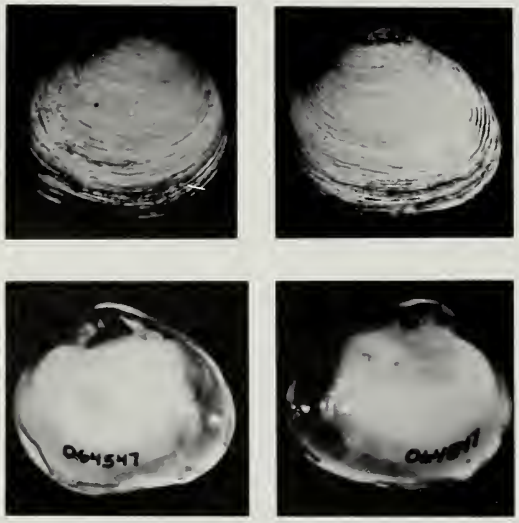

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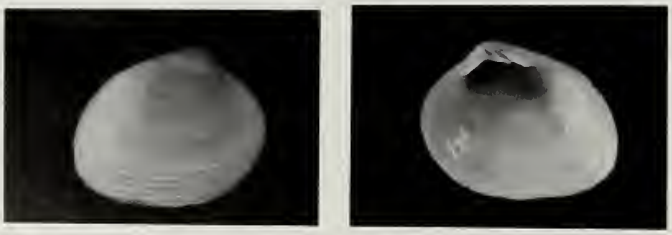

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(SBMNH 34918), Baja California Norte, but not yet found in the eastern Gulf, to Punta Picos, Tumbez Prov., Peru (3°45'S, 80°47'W) (Olsson, 1961); Galápagos Islands, Ecuador: Fernandina (LACM 72-196), Isabela (LACM 34-199), San Salvador (LACM 34-56), and Santa Fé (LACM 71-79). From 10 to 183 m (mean, 49 m), on sand, mud, and rock bottoms, most often the first two. I have examined 192 lots.

This species has been reported from late Pleistocene (Bruff, 1946:233) and early Pleistocene (Arnold, 1903; Clark, 1931:opp. p. 30; Valentine & Meade, 1961:20) strata in southern California.

Remarks: Hertlein & Strong (1949:200, 248–249) differentiated *Semele venusta* from *S. incongrua* on the basis of the former's (1) thicker shell, (2) coarser sculpture ventrally, and (3) attenuated pallial sinus. In addition, I had earlier thought that *S. venusta* was (1) larger, (2) had more prominent beaks, (3) was smoother, with more rounded concentric sculpture, and (4) had darker colors (Coan, 1973:320–321).

After careful study of more abundant material, none of these supposed distinguishing characters holds up. Thick-shelled specimens occur in southern California, and thin-shelled specimens have been obtained from the Gulf of California and the Galápagos Islands. Many of the previously available specimens from southern Mexico and Central America were beachworn and were therefore fairly smooth with rounded sculpture. The pallial sinus criterion does not hold up at all. The largest specimen recorded is from southern California, and the beaks of Panamic specimens are no more prominent that those of some Californian material. Whereas Panamic material is often more colorful, very colorful specimens have also been collected in southern California.

A similar western Atlantic species is *Semele casali* Doello-Jurado, 1949 (Doello-Jurado, 1949:1–4, 8; pl. 1, figs. 1, 2; text fig. 1), which occurs from Surinam to Argentina (Boss, 1972:23–26). It differs in being thicker and in lacking the fine radial sculpture of *S. venusta*.

←

Explanation of Figures 35 to 41

Figures 35–37. *Semele* (*A.*) *venusta* (Reeve). Figure 35: **Lectotype** (herein) of *Amphidesma venustum*; length, 29.0 mm. Figure 36: Lectotype of *S. incongrua* Carpenter; length, 14.1 mm. Figure 37: Holotype of *S. pulchra montereyi* Arnold; length, 18.7 mm.

Figures 38 and 39. *Semele* (*Elegantula*) *rupicola* Dall. Figure 38: Lectotype of *S. rupicola*; length, 22.0 mm. Figure 39: CAS 064547; San Diego, California; length, 39.0 mm.

Figures 40 and 41. *Semele* (*E.*) *rupium* (Sowerby). Figure 40: **Lectotype** (herein) of *Amphidesma rupium*; length, 26.0 mm. Figure 41: Holotype of *S. floreanensis* Soot-Ryen; length, 22.0 mm.

(*Elegantula*) de Gregorio, 1884

(*Elegantula*) de Gregorio, 1884:137.

Type species: *Semela fazisa* de Gregorio, 1884:137–138; by monotypy; =*Amphidesma striata* Reeve, 1853, *ex* Ruppell MS: pl. 7, fig. 46. East Africa and the Red Sea; ?Mediterranean.

This rare species is discussed by Lamy (1913:365–367; pl. 8, figs. 10–12). I have examined only one specimen, a pair from Madagascar, which was, like the type of *Semele fazisa,* collected from a sponge (USNM 719226). The two eastern Pacific species of this subgenus, which nestle in cracks in rock and coral, are often irregular in outline, and have proportionately large hinges.

Semele (*E.*) *rupicola* Dall, 1915

(Figures 38, 39)

Semele rupicola Dall, 1915: Dall, 1915:26; I. Oldroyd, 1925:180; pl. 11, figs. 9, 10; Burch, 1945a:17; 1945b: 17; Keen, 1958:200–201; fig. 495; Coan, 1973:319–320; figs. 5, 16; Bernard, 1983:47.

Semele rupium (Sowerby), *auctt., non* (Sowerby, 1833): Carpenter, 1864b:611, 640, 684 [1872:97, 126, 170]; Williamson, 1892:186; Dall, 1909:272 [in part].

[*non Amphidesma rupium* Sowerby, 1833a:7, 8; pl. 19, figs. 10, 10*—see below].

Semele striosa C. B. Adams, *auctt., non* (C. B. Adams, 1852): Dall, 1915:25–26 [in part]; I. Oldroyd, 1925:179 [in part; not pl. 9, fig. 3, which is a specimen of *S. flavescens*]; Burch, 1945a:17; 1945b:17; 1945c:30; Kanakoff & Emerson, 1959:24.

[*non Amphidesma striosum* C. B. Adams, 1852a:515—see under *Semele pulchra*].

Type material and locality: *S. rupicola*—USNM 272099, lectotype (Coan, 1973:319), left valve; length, 22.0 mm; height, 17.0 mm; convexity, 4.1 mm [pair would be about 8.2 mm] (Figure 38). USNM 663892, paralectotype. Santa Barbara, Santa Barbara Co., California (34°24'N, 119°43'W); W. H. Dall.

Description: Medium-sized (to 71.4 mm; Evans Coll., cited by Draper, 1987:38; Laguna Beach, Orange Co., California); trapezoidal but often irregular in outline from nestling habitat; equivalve; average in thickness; irregularly rounded anteriorly; generally longer, somewhat truncate posteriorly; antero-dorsal margin rounded, with a lunule; postero-dorsal margin straight, with a scarcely evident escutcheon. Periostracum thin, tan. Sculpture of irregular, often wavy concentric ribs and fine radial striae. Externally white; internally generally stained rose to orange on hinge and around valve margins. Pallial sinuses small. Hinge teeth large.

I have illustrated a pair from San Diego, California, that is more characteristic than the type specimen (CAS 064547) (Figure 39).

Distribution: Southeast Farallon Island, San Francisco Co., California (37°4'N, 123°W) (LACM 62-9; CAS

064548), to Punta Entrada, Bahía Magdalena, Baja California Sur (24°32′24″N, 112°4′W) (LACM 71-14). Material labeled as having come from "Cabo San Lucas" (USNM 663893) may be accurate or may represent a labeling error; this record has not been verified in recent years. However, material labeled "Gulf of California" (USNM 130322) probably represents an error. Depth records are from the intertidal zone to 83 m (mean, 15 m). This species lives in rubble, and it can nestle in such rocky sites as empty pholad holes. I have examined 165 lots.

Californian fossil records are from late Pleistocene strata at Cayucos (VALENTINE, 1958:690), Newport Bay (KANAKOFF & EMERSON (1959, as *S.* "*striosa*"), and Point Loma (WEBB, 1937:345); and early Pleistocene strata at San Pedro (VALENTINE & MEADE, 1961:17).

Remarks: Young specimens have a regular shape, regular radial sculpture, and no color. Such material accounts for California records of *Semele striosa* (C. B. Adams).

Semele (*E.*) *rupium* (Sowerby, 1833)

(Figures 40, 41)

Amphidesma rupium Sowerby, 1833: SOWERBY, 1833a:7, 8; pl. 19, figs. 10, 10*; SOWERBY, 1833b:199; HANLEY, 1843:44; 7; pl. 12, fig. 50; 1856:341; REEVE, 1853:pl. 2, fig. 9; CARPENTER, 1857b:182, 304, 359; HANLEY, 1857:pl. 3, figs. 30, 31; TRYON, 1869:122 [*Semele*] [in part]; DALL, 1909:272 [in part]; LAMY, 1913:364 [in part]; DALL, 1915:26; SOOT-RYEN, 1932:314; KEEN, 1958:200–201; fig. 496; KEEN, 1971:254–255; fig. 646; BERNARD, 1983:47.

Semele floreanensis Soot-Ryen, 1932: SOOT-RYEN, 1932:314, 316, 322, 324; pl. 2, figs. 11, 12; CAUQUOIN, 1969:575; KEEN, 1971:255 [as a synonym of *S. rupium*].

Type material and localities: *A. rupium*—BM(NH) 1986083/1, **lectotype (here designated),** the pair illustrated by SOWERBY (1833a) in his fig. 10*; length, 26.0 mm; height, 22.5 mm; convexity, 11.3 mm (Figure 40). BM(NH) 1986083/2, 3, paralectotypes; BM(NH) 1986082/1, paralectotype, the pair illustrated by Sowerby in his figure 10; BM(NH) 1986082/2, 3, additional paralectotypes. I have selected the specimen of Sowerby's "var." because it, and the two paralectotypes in the same lot, are unambiguously associated with the Galápagos Islands (about 0°30′S, 91°W), from "clefts of rocks in coarse gravel"; H. Cuming, 1828–1830. The other specimens look conspecific and probably also came from there, but they were cited as coming from "coarse gravel in the crevices in rocks in coral reefs at Lord Hood's Island." Although there is a Hood Island in the Galápagos [now called Española], there is evidence that Cuming did not visit it (Darwin, as quoted by DANCE, 1986:115), and Cuming twice visited Lord Hood's Island [now called South Marutea] in the Tuamoto Archipelago, where he stayed quite a while (DANCE, 1986:112).

S. floreanensis—Zoologisk Museum, Oslo, Norway 41/10 (31891), holotype, right valve; length, 22.0 mm; height, 17.4 mm; convexity, 4.9 mm [pair would be about 9.8 mm] (Figure 41). Zoologisk Museum, paratype, left valve. Isla Santa María, Galápagos Islands, Ecuador (1°16′S, 90°31′W); A. Wollebaek, 1924–1925.

Description: Small (to 30.7 mm; LACM 38-66; Isla Onslow, Galápagos); trapezoidal, but often irregular in shape due to nestling habitat; equivalve; average in thickness; irregularly rounded to produced anteriorly; longer, somewhat truncate posteriorly; antero-dorsal margin straight to concave, with a lunule; postero-dorsal margin straight, without an escutcheon. Periostracum thin, tan. Sculpture of irregular, sharp concentric ribs, which can be lamellar on posterior margin, and radial threads. White externally, often with red rays; white internally, sometimes with purplish stain posteriorly and on hinge. Pallial sinuses small. Hinge proportionately large.

Remarks: This species differs from *Semele rupicola* in having a more quadrate outline, with more anterior beaks, a thinner shell, more regular sculpture, being more brightly colored, and in having a less projecting resilifer.

Distribution and habitat: Galápagos Islands: Baltra (CAUQUOIN, 1969), Bartolomé (SBMNH 34920), Fernandina (LACM 66-125), Isabela (CAS 064558), Onslow (LACM 38-66), Plazas (UCMP B.3603), San Cristóbal (ANSP 153334), San Salvador (LACM 34-52; UCMP B.3621, B.3625), Santa Cruz (SBMNH 34900, 34919; CAS 064549, 064551; UCMP B.3618; USNM 752918), and Santa María (TOMLIN, 1928:197; SOOT-RYEN, 1932: 314, and type location of *Semele floreanensis*); and Isla del Coco, Costa Rica (SBMNH 34937 and several other lots). From 1 to 73 m (mean, 17 m), on coral rubble substrates. I have examined 31 lots.

DALL (1909:272) reported this species from Guayaquil, Ecuador, but there are no specimens in collections to support this.

HERTLEIN & STRONG (1939:369) report this species from late Pleistocene strata on Isla San Salvador.

Remarks: SOOT-RYEN (1932) does not compare his new *Semele floreanensis* with *S. rupium,* which he also reports from Isla Santa María. *Semele floreanensis* is merely a young specimen that is regular in shape.

There is no evidence that members of this subgenus occur in the Indo-Pacific province between east Africa and the Galápagos Islands. *Semele crenata* A. ADAMS & ANGAS, 1864:426, described from Moreton Bay, Queensland, Australia, was compared to *S. rupium* and was said to differ in having crenate concentric ribs. However, it is now regarded as a synonym of *S. crenulata* (REEVE, *ex* Sowerby MS, 1853:pl. 2, fig. 8), a very dissimilar species with more evenly rounded shells. I have seen a specimen of this species from the type locality of *S. crenata* (Australian Mus. C-76966).

(*Semele*), *s.l.*

Group of *Semele barbarae* (Boone)

This New World lineage was diverse in the Tertiary of the Caribbean but now survives only in the eastern Pacific. The stem may be *Semele chipolana* Dall, 1900 (DALL, 1900: 986–987, 1193; pl. 37, fig. 3) from the early Miocene Chipola Formation of Florida, as first concluded by GARDNER (1928:203). This species is perhaps closest to the Recent eastern Pacific *S. jovis* (Reeve), but it is thinner, more elongate, and more equilateral. *Semele claytoni* Maury, 1917 (MAURY, 1917:391–392, 413; pl. 35, fig. 9) of the late Miocene Cercado Formation of the Dominican Republic and *S. claytoni couvensis* Maury, 1925 (MAURY, 1925:270–271; pl. 21, fig. 4) of the late Miocene of Trinidad may represent the ancestors of the Recent eastern Pacific *S. barbarae* (Boone) and the Plio-Pleistocene western Atlantic *S. perlamellosa* Heilprin, 1887.

Another branch of this lineage leads to *Semele leana* Dall of the late Pliocene Caloosahatchee Formation of Florida, which I regard as a synonym of the Recent eastern Pacific *Semele rosea* (Sowerby) (see under same).

Semele barbarae (Boone, 1928)

(Figures 42–44)

Tellina barbarae Boone, 1928: BOONE, 1928:9; pl. 1, upper fig.; HERTLEIN & STRONG, 1949:244 [as a synonym of *S. jovis*]; KEEN, 1958:196 [as a possible synonym of *S. jovis*]; KEEN, 1971:251 [as a possible synonym of *S. jovis*]; BERNARD, 1983:46 [as a synonym of *S. jovis*].

Amphidesma purpurascens Sowerby, 1833, *non* (Gmelin, 1791), *non* Lamarck, 1818: SOWERBY, 1833a:8; pl. 18, fig. 5; SOWERBY, 1833b:199–200; REEVE, 1841:68; pl. 48, fig. 5; HANLEY, 1843:44; 7; pl. 12, fig. 45; 1856:341; REEVE, 1853:pl. 6, fig. 37; HANLEY, 1857:pl. 3, figs. 28, 29; TRYON, 1869:121 [*Semele*]; DALL, 1909:272.

[*non Venus purpurascens* Gmelin, 1791, a *Semele* (see above)].

[*non Amphidesma purpurascens* LAMARCK, 1818:493, which has been synonymized by most authors with *Ervilia nitens* (Montagu, 1808)].

Semele sowerbyi Lamy, 1912, new name for *Amphidesma purpurascens* Sowerby, 1833, *non* (Gmelin, 1791), *non* Lamarck, 1818; *non Semele sowerbyi* Tryon, 1869: LAMY, 1912:165, footnote; LAMY, 1913:328, 352, footnotes; HERTLEIN & STRONG, 1949:248, footnote; OLSSON, 1961: 360, 367, 538; pl. 65, figs. 7, 7a; CAUQUOIN, 1969:577; KEEN, 1971:255–256; fig. 648; BERNARD, 1983:47.

[*non Semele sowerbyi* TRYON, 1869:122; see under it].

Type material and localities: *T. barbarae*—Original lost or mislaid during transfer of the Bingham Oceanographic Collection to the Peabody Museum of Natural History at Yale University, probably never to be found (W. O. Hartman, in correspondence, 15 May 1986). The original specimen measured approximately 36 mm in length and 27 mm in height (Figure 42). Archipiélago de las Perlas, Panama, 22 m; H. P. Bingham, 31 March–2 April 1926. USNM 588133, **neotype (here designated),** pair; length, 47.4 mm; height, 36.3 mm; convexity, 13.0 mm (Figure 43). Isla San José, Archipiélago de las Perlas, Panama (about 8°15′N, 79°5′W), beach drift; J. P. E. Morrison, 15 March 1944.

A. purpurascens Sowerby—BM(NH) 1986080, holotype, left valve; length, 48.5 mm; height, 37.3 mm; convexity, 7.8 mm [pair would be about 15.6 mm] (Figure 44). Santa Elena, Guayas Prov., "W. Col." [Ecuador] (2°12′S, 80°52′W), on beach; H. Cuming, 1828–1830.

Description: Medium-sized (to 48.5 mm; holotype of *Amphidesma purpurascens* Sowerby); elongate; equivalve, compressed; shells thin for size; approximately equilateral; rounded anteriorly; produced, truncate posteriorly (some specimens more rounded); antero-dorsal margin straight, with a narrow lunule; postero-dorsal margin straight, with an escutcheon. Periostracum thin, brown. Sculpture of thin, closely spaced concentric ribs that lean dorsally throughout the surface (less so than in *Semele jovis*), sometimes broken into frills. Color purple throughout, with a long, narrow white radial ray from the beaks; purple within; hinge white. Pallial sinuses medium in size.

Distribution and habitat: Bahía Isla Grande, Guerrero, Mexico (17°40′N, 101°39′W) (LACM 124463; SBMNH 34921), to Playas, Guayas Prov., Ecuador (2°39′S, 80°23′W) (Skoglund Coll.). Depths from 27 to 101 m (mean, 54 m). No substrates recorded. Uncommon; I have examined only 11 lots.

HOFFSTETTER (1952: 41) reports this species as a "subfossil" on the Santa Elena Peninsula, Ecuador.

Remarks: Before I realized that *Semele sowerbyi* Lamy, 1912, was a junior homonym of *S. sowerbyi* Tryon, 1869, I debated somewhat inconclusively whether to synonymize *Tellina barbarae* Boone, with the former or with *S. jovis* (Reeve). Boone's type is lost; the description lacks critical details; and the figure could depict either species. It was not important to resolve the question because it would have been a synonym in either case.

The arguments in favor of its placement with *Semele jovis* were its rounded outline, Boone's description of it as being rosy purple, and its somewhat expanded antero-dorsal margin. On the other hand, *S. jovis* is not yet known from south of Costa Rica; the specimens reported as *S. jovis* from the Archipiélago de las Perlas by HERTLEIN & STRONG (1955b:201–202) are instead the present species (AMNH 73613). Moreover, rare specimens of the present species may be rounded, as, for example, that illustrated by OLSSON (1961:pl. 65, figs. 7, 7a), which I recently verified (PRI 25835). Now, with the pressing need for a substitute for the junior homonym *S. sowerbyi* Lamy, it is important to establish the identity of *Tellina barbarae*, which I do here by means of a neotype designation.

Semele barbarae (as *S. sowerbyi* Lamy) was compared by OLSSON (1961) to *S. perlamellosa* Heilprin (HEILPRIN, 1887:

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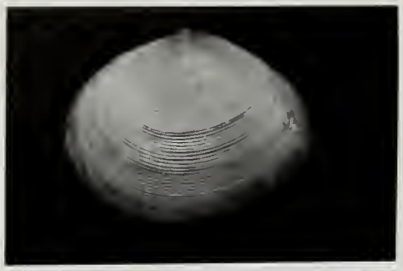

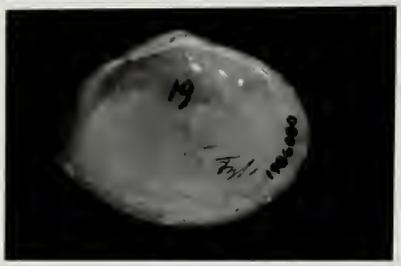

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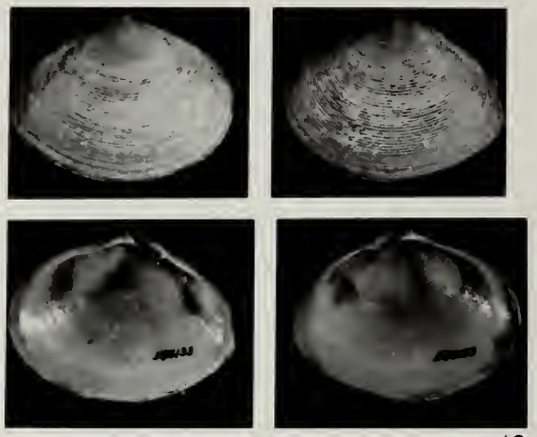

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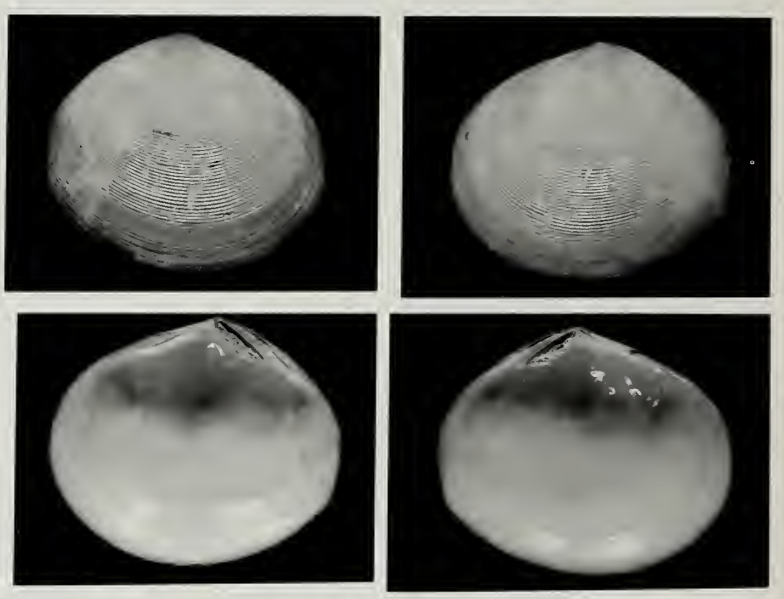

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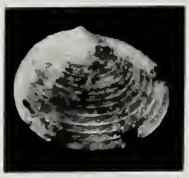

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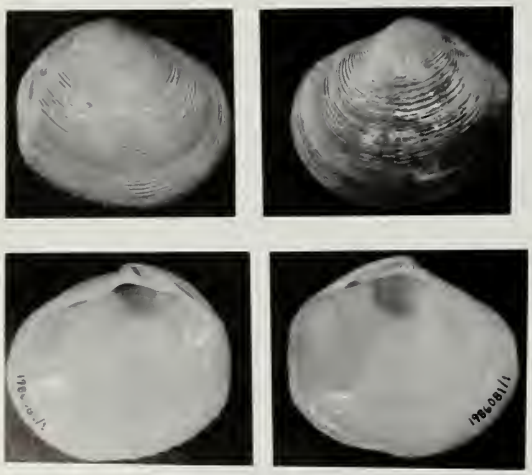

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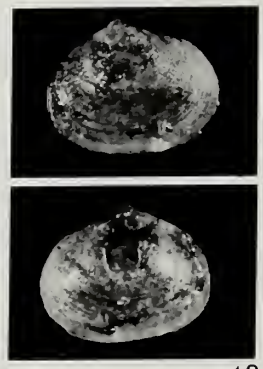

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92, 102; pl. 2, fig. 23) from late Pliocene and early Pleistocene strata in Florida. The latter is more elongate, with heavier sculpture of more widely spaced concentric ribs. Its posterior end is more broadly set off, and it attains a much larger size (88.7 mm in one specimen I examined; TU Loc. 726).

Semele jovis (Reeve, 1853, *ex* A. Adams MS)

(Figures 45, 46)

Amphidesma jovis Reeve, 1853, *ex* A. Adams MS: Reeve, 1853:pl. 5, fig. 34 [as "A. Adams"]; A. Adams, 1854: 94 [*Semele*]; Tryon, 1869:120; Lamy, 1913:357, footnote; Dall, 1915:26; Hertlein & Strong, 1949:240, 244–245; Keen, 1958:196–197; fig. 485; Olsson, 1961: 360, 367–368, 539, 558; pl. 66, fig. 12; pl. 85, figs. 7, 7a; Keen, 1971:251–252; fig. 633; pl. 8, fig. 5; Bernard, 1983:46; Gemmell *et al.*, 1987:55–56.

?*Tellina lamellata* Carpenter, 1857: Carpenter, 1857b:245 [*nomen nudum*]; Carpenter, 1857c:37; Keen, 1958:168–169; fig. 388; Keen, 1968:394–395, 400; figs. 20a, b [as *Semele* sp.]; Keen, 1971:250 [as *Semele* sp.]; Bernard, 1983:46 [as a synonym of *S. jovis*].

Type material and localities: *A. jovis*—BM(NH) 1986071, holotype, pair; length, 58.3 mm; height, 48.9 mm; convexity, 22.9 mm (Figure 45). Original locality unknown. Hertlein & Strong (1949:244) designated Puerto Parker, Guanacaste Prov., Costa Rica (10°56′N, 85°48′W), as the type locality.

T. lamellata—BM(NH) 1857.6.4.121, **lectotype (here designated),** pair; length, 3.3 mm; height, 2.5 mm; convexity, 0.76 mm (Figure 46). Paralectotypes, two valves on the same slide. Mazatlán, Sinaloa, Mexico (23°12′N, 106°24′W); "nestling on *Chama* and *Spondylus*"; F. Reigen, 1848–1850.

Description: Medium-sized (length to 71.4 mm; SDNHM 31223; La Paz, Baja California Sur, Mexico); rounded; inflated, left valve somewhat more so; shells average in thickness; longer, rounded anteriorly; slightly truncate posteriorly; antero-dorsal margin convex, concave near beaks, with a narrow, elongate lunule; postero-dorsal margin convex, with an elongate escutcheon. Periostracum thin, tan. Sculpture of regular, thin concentric ribs that lean dorsally. Color light pink externally, with a narrow white rib radiating a short distance from beaks, bracketed with broad, reddish brown areas (rare all-white specimens have been collected); white to pink internally; hinge white. Pallial sinuses medium in size.

An external view of a living animal was given by Keen (1971:pl. 8, fig. 5).

Distribution and habitat: Bahía Adair, Sonora, Mexico (31°30′N, 113°37′W) (LACM 124459), throughout the Gulf of California, to Bahía Ballena, Puntarenas Prov., Costa Rica (9°44′12″N, 84°59′32″W) (LACM 72-45). Intertidal zone to 55 m (mean, 21 m), on sand and perhaps mud. I have examined 46 lots.

Remarks: The type material of *Tellina lamellata* consists of one tiny closed pair and two still smaller valves, all glued to a glass slide. Keen (1968) concluded from one of the open valves that they were juvenile *Semele*. The material has since been removed and reglued, and the hinge details are not clearly visible. However, the sculpture and shape are not unlike juvenile *Semele*. I have compared these specimens with the few juvenile specimens available for study of several species of *Semele* and conclude that this placement is the most likely. Unfortunately, there are no other available specimens of *S. jovis* as small as these.

Semele jovis is very close to *S. barbarae*. It differs in its generally more oval outline; thicker shell; less produced and truncate posterior end; less frilly concentric sculpture; rosy rather than purple color; and shorter, broader white band radiating from the beaks.

Semele rosea (Sowerby, 1833)

(Figures 47–50)

Amphidesma roseum Sowerby, 1833: Sowerby, 1833a:7, 8; pl. 17, fig. 1; Sowerby, 1833b:199; Reeve, 1841:67; pl. 47, fig. 1; Hanley, 1843:44; 7; pl. 12, fig. 35; 1856:341; Reeve, 1853:pl. 3, fig. 17; Hanley, 1857:pl. 3, fig. 26; Tryon, 1869:119 [*Semele*; as a synonym of *S. decisa*]; Dall, 1909:272; Lamy, 1913:356–357; Hertlein & Strong, 1949:244–245; Olsson, 1961:360, 366–367, 537; pl. 64, fig. 8; Cauquoin, 1969:576–577; Keen, 1971:253–255; fig. 644, 645; Bernard, 1983:47.

?*Tellina regularis* Carpenter, 1857: Carpenter, 1857b:245 [*nomen nudum*]; Carpenter, 1857c:36–37; Keen, 1958: 177 [*nomen dubium*]; Brann, 1966:13, 32; pl. 7, fig. 57; Keen, 1968:394, 395, 400; fig. 21 [juv. *Semele*]; Keen, 1971:250 [juv. *Semele*].

Semele junonia Verrill, 1870: Verrill, 1870:217–218; Lamy, 1913:356–357 [as a variety of *S. rosea*]; Dall, 1915:26; Keen, 1958:198; pl. 4; Cauquoin, 1969:576 [as a possible synonym of *S. rosea*]; Keen, 1971:251–252; fig. 634; pl. 4; Bernard, 1983:46.

Semele leana Dall, 1900: Dall, 1892:211 [*nomen nudum*]; Dall, 1900:992, 1193; pl. 37, figs. 1, 2.

Semele tabogensis Pilsbry & Lowe, 1932: Pilsbry & Lowe, 1932:91–92, 144; pl. 12, figs. 5, 5a, 5b; Hertlein &

←

Explanation of Figures 42 to 50

Figures 42–44. *Semele barbarae* (Boone). Figure 42: Original figure of *Tellina barbarae*; specimen length, 36 mm. Figure 43: **Neotype** (herein) of *T. barbarae*; length, 47.4 mm. Figure 44: Holotype of *Amphidesma purpurascens* (Sowerby) (*non* (Gmelin); *non* Lamarck); length, 48.5 mm.

Figures 45 and 46. *Semele jovis* (Reeve). Figure 45: Holotype of *Amphidesma jovis*; length, 58.3 mm. Figure 46: **Lectotype** (herein) of *Tellina lamellata* Carpenter; length, 3.3 mm.

Figures 47–50. *Semele rosea* (Sowerby). Figure 47: Specimen figured by Reeve (1853) from type lot; length, 64.8 mm. Figure 48: **Lectotype** (herein) of *Tellina regularis* Carpenter; length, 1.8 mm. Figure 49: **Lectotype** (herein) of *S. junonia* Verrill; length, 64.6 mm. Figure 50: Holotype of *S. tabogensis* Pilsbry & Lowe; length, 36.8 mm.

STRONG, 1949:240, 248; KEEN, 1958:200–201; fig. 500; OLSSON, 1961:360, 366–367, 537; pl. 64, fig. 7 [as a subspecies of *S. rosea*; vice versa on p. 537]; CAUQUOIN, 1969:576 [as a synonym of *S. rosea*]; KEEN, 1971:254–255; fig. 645 [as a subspecies of *S. rosea*]; BERNARD, 1983:47 [as a synonym of *S. rosea*]; HERTZ, 1986:41.

Type material and localities: *A. roseum*—Sowerby's holotype, a left valve, is missing. It measured 63.2 mm in length, 58.4 mm in height; his measurement of 27.9 mm in convexity would presumably have represented a pair. I here illustrate BM(NH) 1986081/1, the pair figured by REEVE (1853), apparently from the type lot; length, 64.8 mm; height, 55.6 mm; convexity, 26.9 mm (Figure 47). Tumbez, Tumbez Prov., Peru (3°29′S, 80°23′W); H. Cuming, 1828–1830.

T. regularis—BM(NH) 1857.6.4.120, **lectotype (here designated),** the intact right valve glued on the slide; length, 1.8 mm; height, 1.5 mm; thickness, 0.35 mm [very hard to measure; pair would be about 0.7 mm] (Figure 48). Paralectotype, broken left valve on the same slide, possibly mate to right valve. Mazatlán, Sinaloa, Mexico (23°12′N, 106°24′W); "from *Spondylus* washings"; F. Reigen, 1848–1850.

S. junonia—Peabody Museum 4080, **lectotype (here designated),** pair; length 64.6 mm; height, 56.0 mm; convexity, 27.8 mm (Figure 49). Near La Paz, Baja California Sur (about 24°10′N, 110°19′W); from pearl divers by J. Pederson. This was one of six original pairs. Only one other valve, now a paralectotype, remains in the collection.

S. leana—USNM 155790, 8 syntypes (1 pair, 7 valves) (not figured here). Caloosahatchie Formation at Caloosahatchie River and Shell Creek, Florida; late Pliocene.

S. tabogensis—ANSP 155012, holotype, right valve; length, 36.8 mm; height, 29.6 mm; convexity, 5.0 mm [pair would be about 10.0 mm] (Figure 50). SDMNH 50770, paratypes, 3 valves. Isla Taboga, Panama (about 8°47′N, 79°34′W); "among rocks near the bathing beach"; H. N. Lowe, 1931.

Description: Large (length to 84.8 mm; Swoboda Coll.; Bahía San Carlos, Sonora); rounded; left valve more inflated; average in thickness; longer, rounded anteriorly; truncate posteriorly; antero-dorsal margin convex, with a lunule; right valve with anterior and posterior dorsal flanges that overlap left valve; postero-dorsal margin convex, with a narrow escutcheon. Periostracum thick, dark brown, shiny. Sculpture of narrow concentric ribs that lean dorsally, more numerous in right valve. Externally pink to orange, darker at beaks; pink within. Pallial sinuses medium in size.

Distribution and habitat: Northern entrance of Bahía Magdalena, Baja California Sur (24°32′N, 112°4′W) (LACM 71-14), into the Gulf of California as far north as Bahía de los Angeles, Baja California Norte (28°55′N, 113°31′W) (SBMNH 34924), and Bahía San Carlos, Sonora (27°56′N, 111°4′W) (LACM 64-36; Skoglund Coll.; Poorman Coll.), Mexico, southward to Tumbez, Tumbez Prov., Peru (3°29′S, 80°23′W) (type locality). Other than a lot labeled "Peru" (ANSP 51760), the most southerly station from which I have seen material is Playas, Guayas Prov., Ecuador (Skoglund Coll.). Depth records are from the intertidal zone to 113 m (mean, 23 m). Substrates are indicated for only 4 lots: 3 sand and 1 rocky. I have examined 40 lots.

HOFFSTETTER (1948:80) noted this species from Pleistocene strata on the Santa Elena Peninsula, Ecuador.

Remarks: Carpenter's *Tellina regularis,* like his *T. lamellata,* was based on juvenile specimens of *Semele* (and should never have been given a name). The lack of comparative material of equivalent size prevents definite placement, but it seems to come closest to young *S. rosea,* which occurs at Mazatlán (SDNHM 84561).

VERRILL (1870) differentiated *Semele junonia* from *S. rosea* on the grounds that it was more orbicular and had more concentric ribs. The lectotype of *S. junonia* has virtually the same length-height ratio (1.15) as does the Reeve specimen from the original lot of *S. rosea* (1.17), and Sowerby's original specimen was even slightly higher for its length (1.09). Both Sowerby's and Reeve's figures depict left valves, which have fewer concentric ribs than right valves. KEEN (1971:251–252, 253–255) lists the two as separate taxa but without differentiating characters.

Semele leana Dall, from the late Pliocene Caloosahatchie Formation of Florida, proves to be identical to *S. rosea.* It shows the same range of variability as Recent material—some elongate anteriorly, some more rounded; some with a narrowly restricted posterior slope, some with a more broadly defined area (based on study of TU material).

PILSBRY & LOWE (1932) did not list any characters to separate their *Semele tabogensis* from *S. rosea.* OLSSON (1961) made the two subspecies, listing both from Venado Beach, Panama. (In his text, *S. tabogensis* is a subspecies of *S. rosea*; in his plate explanation, it was reversed.) He says that *S. r. tabogensis* is more subovate, its posterior end longer, and its color more uniform, characters well within the range of variability of *S. rosea.*

Group of *Semele guaymasensis*

Small, with conspicuous radial sculpture at least on ends of valves, evidently occurring on sand bottoms, mostly offshore.

Semele guaymasensis Pilsbry & Lowe, 1932

(Figures 51, 52)

Semele guaymasensis Pilsbry & Lowe, 1932: PILSBRY & LOWE, 1932:92, 144; pl. 12, figs. 8, 9; HERTLEIN & STRONG, 1949:240, 243–244; KEEN, 1958:196–197; fig. 483; OLSSON, 1961:361, 369 [in part], 538; pl. 65, fig. 4 [539; pl. 66, fig. 6; =*S. verrucosa* Mörch]; KEEN, 1971:251–252; fig. 632; COAN, 1973:325; GEMMELL *et al.,* 1980: 35; fig. 15; BERNARD, 1983:46; HERTZ, 1986:38; GEMMELL *et al.,* 1987:55.

Type material and locality: ANSP 155011, **lectotype (here designated),** right valve; length, 15.9 mm; height, 12.3 mm; convexity, 2.3 mm (Figure 51). ANSP 361643, paralectotype, left valve; length, 16.1 mm; height, 12.0 mm; convexity, 2.7 mm (Figure 52). PILSBRY & LOWE (1932) said that only unpaired valves were collected, but they illustrated as the "type" two opposite valves of similar size from different individuals. SDNHM 50772, paratypes, 3 valves. Guaymas, Sonora, Mexico (27°55′N, 110°53′W); 37 m; H. N. Lowe, Jan. 1930.

Description: Small (length to 27.8 mm; CAS 064675; Estero Soldado, Sonora, Mexico); oblong; equivalve; shells average in thickness; longer, sharply rounded anteriorly; somewhat truncate posteriorly; antero-dorsal margin straight, with a lunule; postero-dorsal margin straight, with an escutcheon, largest in left valve. Periostracum very thin, tan. Sculpture of concentric ribs that form a carina along escutcheon in many specimens. Anterior slope with 4–6 heavy radial ribs in each valve. Externally whitish, with flecks or rays of purple; dorsal margin with purplish blotches; white internally, with purple patches in some specimens; hinge purple. Pallial sinuses large.

Distribution and habitat: From La Paz, Baja California Sur (24°10′N, 110°19′W) (USNM 555455, and several other lots; LACM 66-30; CAS 064550, 064552, 064555), northward throughout the Gulf of California to its head at Puerto Peñasco, Sonora (about 31°20′N, 113°40′W) (SBMNH 34922, 34923; UCMP E.8323; CAS 064553; ANSP 164508), and south to Bahía Chamela, Jalisco, Mexico (19°32′N, 105°6′W) (LACM 127520). From the intertidal zone to 110 m (mean, 16 m), on sand and mud; intertidal zone on sand bars (GEMMELL *et al.*, 1987:55). I have examined 136 lots.

Records of this species from Panama (STRONG & HERTLEIN, 1939:184; OLSSON, 1961:369, 539; pl. 66, fig. 6) were based on specimens of *Semele verrucosa* Mörch. A single lot labeled "Redondo Beach," California (MCZ 105544), is undoubtedly the result of mixing in shipment.

This species has been reported from Pleistocene formations at Bahía Magdalena, Baja California Sur (JORDAN, 1936:112, 145–146), and at Puerto Peñasco, Sonora (HERTLEIN & EMERSON, 1956:165).

Remarks: As pointed out by HERTLEIN & STRONG (1949: 244), this species is close to *Semele anteriocosta* Vokes (VOKES, 1938:13–15; fig. 5) from strata of late Miocene age on Trinidad; JUNG (1969:398–399, 611; pl. 36, figs. 4–9) reports "*S. aff. anteriocosta*" from an early Pliocene formation on that island.

Semele pulchra (Sowerby, 1832)

(Figures 53–55)

Amphidesma pulchrum Sowerby, in Broderip & Sowerby, 1832: SOWERBY, in Broderip & Sowerby, 1832:57; SOWERBY, 1833a:7, 8; pl. 17, figs. 2, 2*; REEVE, 1841: 67; pl. 47, figs. 2, 2*; HANLEY, 1843:45; 6; pl. 12, fig. 6; 1856:341; C. B. ADAMS, 1852a:514–515 [1852b:290–291]; REEVE, 1853:pl. 1, fig. 2; CARPENTER, 1857b:188, 280, 303 [*Semele*]; HANLEY, 1857:pl. 3, figs. 23, 24; CARPENTER, 1864a:367 [1872:203]; CARPENTER, 1864b: 537, 553, 592, 611, 640, 668 [1872:23, 39, 78, 97, 126, 154]; TRYON, 1869:121; ARNOLD, 1903:166, 392; pl. 15, figs. 1, 1a; DALL, 1909:272; LAMY, 1913:353–354; DALL, 1915:27; I. OLDROYD, 1925:181; GRANT & GALE, 1931: 377; BURCH, 1945a:18; 1945b:17; HERTLEIN & STRONG, 1949:240, 258; pl. 1, fig. 15; KEEN, 1958:198–199; fig. 492; OLSSON, 1961:361, 368–369, 538; pl. 65, fig. 5; KEEN, 1971:253–254; fig. 641; COAN, 1973:321–323; figs. 8–11, 18; BERNARD, 1983:47.

Amphidesma striosum C. B. Adams, 1852: C. B. ADAMS, 1852a:515, 547 [1852b:291, 323]; CARPENTER, 1857b: 280, 303 [*Semele*]; CARPENTER, 1864a:367 [1872:203] [similar to *S. pulchra*]; CARPENTER, 1864b:553 [1872: 39]; TRYON, 1869:122; LAMY, 1913:354, 365, footnotes; I. OLDROYD, 1925:179 [in part]; not pl. 9, fig. 3 [=*S. flavescens*]; TURNER, 1956:90, 128–129; pl. 18, figs. 1, 2; KEEN, 1958:200–201; fig. 499; OLSSON, 1961:363–364 [as a synonym of *S. lenticularis*]; KEEN, 1971:250 [as a synonym of *S. bicolor*].

[Not to be confused with *Semele striata* (Reeve, 1853), type species of *Elegantula*; see above.]

?*Mesodesma rubrotincta* Gould, 1857, *ex* "Sowerby" MS [*nomen nudum*; probably a misspelling of *Amphidesma rubrolineatum* Conrad, but *non* Conrad, 1837 (see under *S. decisa*)]: GOULD, 1857:330; CARPENTER, 1864b:592 [1872:78]; LAMY, 1913:354, 364, footnotes.

[*non* CONRAD, 1837:239; pl. 18, fig. 11].

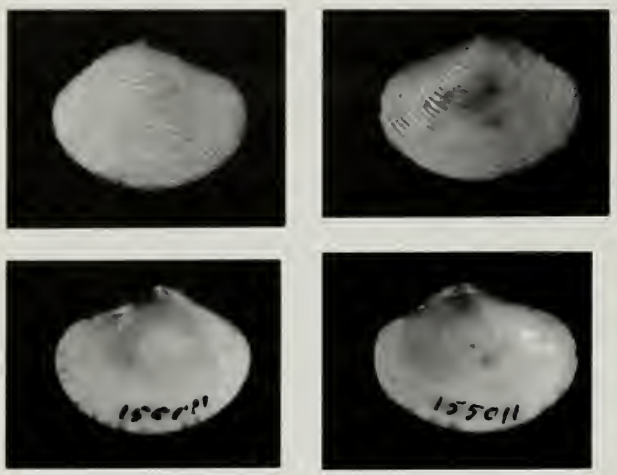
Semele quentinensis Dall, 1921: DALL, 1921:22; DALL, 1925: 26, 36; pl. 8, fig. 4; GRANT & GALE, 1931:377; HERTLEIN & STRONG, 1949:240, 246–247, 258; pl. 1, fig. 10; KEEN, 1958:199; fig. 494; OLSSON, 1961:361; KEEN, 1971:253–254; fig. 643 [as a possible synonym of *S. pulchra*]; COAN, 1973:321 [as a synonym of *S. pulchra*].

Type material and localities: *A. pulchrum*—BM(NH) 1973087/1, lectotype (COAN, 1973:322), pair; length, 29.0 mm; height, 21.6 mm; convexity, 11.1 mm (Figure 53). BM(NH) 1973087/2, 3, paralectotypes, 2 smaller pairs. Bahía de Caráquez, Guayas Prov., Ecuador (0°35′S, 80°25′W); H. Cuming, 1828–1830.

A. striosum—MCZ 186542, holotype, right valve; length, 21.3 mm; height, 17.9 mm; convexity, 3.6 mm [pair would be about 7.2 mm] (Figure 54). Panama, presumably near Panama City (about 8°58′N, 79°32′W); C. B. Adams, 27 Nov. 1850–2 Jan. 1851. (See discussion below.)

S. quentinensis—USNM 333114, lectotype (COAN, 1973: 322), right valve; length, 23.9 mm; height, 18.2 mm; convexity, 4.1 mm [pair would be about 8.2 mm] (Figure 55). USNM 645416, paralectotypes, 4 valves. Bahía San Quintín, Baja California Norte (about 30°26′N, 115°56′W); C. R. Orcutt, Nov. 1888.

Description: Small (length to 31.9 mm; Skoglund Coll.; Isla Venado, Panama); oblong; equivalve; shells average in thickness; longer, sharply rounded anteriorly; somewhat truncate posteriorly; antero-dorsal margin straight, with a lunule; postero-dorsal margin straight, with an escutch-



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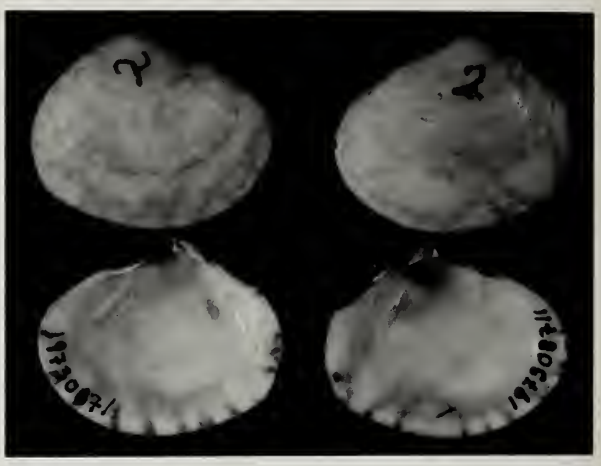

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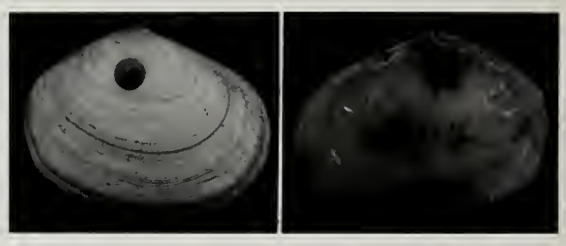

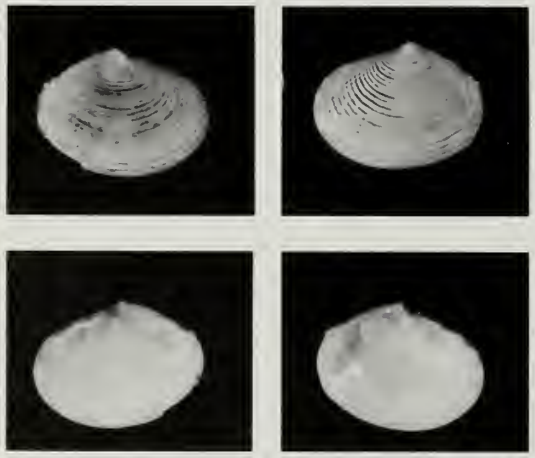

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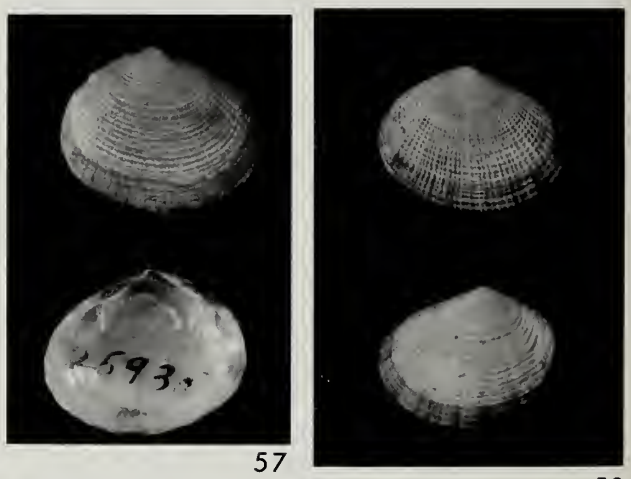

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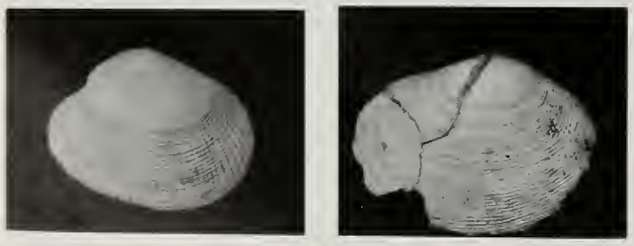

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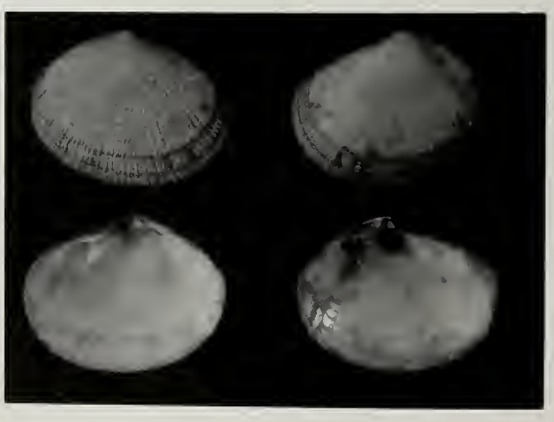

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eon. Periostracum thin, light tan. Sculpture of very fine concentric ribs and fine radial rays on anterior slope in both valves. White externally, with purple flecks and rays; white internally, with a suffusion of purple, pink, or yellow; hinge dark purple. Pallial sinuses large.

Distribution and habitat: Mugu Lagoon, Ventura Co., California (34°6′N, 119°6′W) (BURCH, 1945a:18); Catalina Island, Los Angeles Co., California (about 33°27′N, 118°28′W) (USNM 194333), southward, but not into the Gulf of California farther north than La Paz, Baja California Sur (24°10′N, 110°19′W) (USNM 150835), and Mazatlán, Sinaloa (23°12′N, 106°24′W) (SBMNH 20993), Mexico, to Zorritos, Tumbez Prov., Peru (3°40′S, 80°34′W) (OLSSON, 1961). I have not seen Olsson's material but there is no reason to doubt this record, and I have seen material from about 1° latitude north of Zorritos at Estero Salitro, Ecuador (CAS 064538). Three lots labeled as having come from Monterey, Monterey Co., California (36°31′N, 121°53′W) (LACM 57172; CAS 064556; ANSP 51756), may either represent the result of larval settlement in an unusually warm year or labeling errors; no populations have been noted there in recent years. From the intertidal zone to 110 m (mean, 15 m), on both mud and sand substrates. I have examined 115 lots.

According to FINÉT (1985:42) this species was recorded from the Galápagos Islands, but he doubts the record, and I have seen no material from there.

This species has been reported in strata of late Pleistocene age from Anacapa Island, Santa Barbara Co., California (VALENTINE & LIPPS, 1963:1294), to Bahía Magdalena, Baja California Sur (JORDAN, 1936:112), with many intermediate records. It has also been recorded in early Pleistocene deposits from the San Pedro, Los Angeles Co., area (for example, SCHENCK, 1945:513).

Remarks: The identity of *Amphidesma striosum* C. B. Adams has long been controversial. OLSSON (1961:364) claimed that Adams' real type had been lost,[2] and he decided on the basis of the original description that the taxon was a synonym of *Semele lenticularis* (with which he also synonymized Adams' *A. bicolor*). He recognized that the specimen thought to be the type of *A. striosum* by CARPENTER (1864a, b), TURNER (1956), and KEEN (1958) was a stray valve of *S. pulchra,* a species also reported by C. B. ADAMS (1852:514–515) from Panama.

C. B. Adams himself provided few clues. *Amphidesma striosum* is not compared with any of the other species possibly involved—all of which he had before him—*A. pulchrum, A. bicolor,* and *Semele lenticularis* (as *A. ventricosum* C. B. Adams), and I see little in their descriptions to make a convincing case in favor of any interpretation. The presumed type specimen **can** be construed to match the original description, though the prominent radial sculpture is confined to the anterior end, a fact not mentioned by Adams. The measurements given by Adams are a reasonable match. (His stated measurements were 19.8 mm long, 18.0 mm high, 8.4 mm in convexity; the holotype is 21.3 mm long, 17.9 mm high, and, if both valves were present, about 7.2 mm in convexity.) Other measurements by Adams of his specimens were as far off. In any case, *A. striosum* would end up in synonymy.

Records of *Semele striosa* from California (for example, BURCH, 1945a:17) were based on young specimens of *S. rupicola.*

DALL (1921) did not compare his fossil *Semele quentinensis* with the Recent *S. pulchra.* HERTLEIN & STRONG (1949) recognized *S. quentinensis* from the Recent fauna as a northern species (California to Costa Rica), differing from the southern *S. pulchra* (Nicaragua to Peru) in being (1) more elongate, (2) thinner, (3) lighter in color, and (4) having a more gently sloping antero-dorsal margin. However, variability within this species easily accounts for these supposed differences.

Semele verrucosa Mörch, 1860

Semele verrucosa verrucosa Mörch, 1860

(Figures 56–58)

Semele verrucosa Mörch, 1860: MÖRCH, 1860:190–191 [as *S.* (*Amphidesma*)]; KEEN, 1966b:12, 13, 16–17; figs. 17a, b; KEEN, 1971:255–256; fig. 652; BERNARD, 1983:47.

[*non Semele verrucosa* Mörch, *auctt.,* =*S. formosa* (Sowerby)].

Semele margarita Olsson, 1961: OLSSON, 1961:360, 370, 539; pl. 66, fig. 3; KEEN, 1966b:16–17 [as possible synonym of *S. verrucosa*]; KEEN, 1971:255 [as a synonym of *S. verrucosa*].

Semele guaymasensis Pilsbry & Lowe, *auctt., non* Pilsbry & Lowe, 1932: OLSSON, 1961:369 [in part], 539; pl. 66, fig. 6.

[*non* PILSBRY & LOWE, 1932:144; pl. 12, figs. 8, 9].

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Explanation of Figures 51 to 61

Figures 51 and 52. *Semele guaymasensis* Pilsbry & Lowe. Figure 51: **Lectotype** (herein) of *S. guaymasensis*; length, 15.9 mm. Figure 52: ANSP 361643, paralectotype; length, 16.1 mm.

Figures 53–55. *Semele pulchra* (Sowerby). Figure 53: Lectotype of *Amphidesma pulchrum*; length, 29.0 mm. Figure 54: Holotype of *A. striosum* C. B. Adams; length, 21.3 mm. Figure 55: Lectotype of *S. quentinensis* Dall; length, 23.9 mm.

Figures 56–58. *Semele verrucosa verrucosa* Mörch. Figure 56: Lectotype of *S. verrucosa*; length, 10.6 mm. Figure 57: Holotype of *S. margarita* Olsson; length, 14.0 mm. Figure 58: CAS 064536; Playas del Coco, Costa Rica; length, 17.5 mm.

Figures 59–61. *Semele verrucosa pacifica* Dall. Figure 59: Holotype of *S. pacifica*; length, 18.2 mm. Figure 60: Holotype of *S. jaramija* Pilsbry & Olsson; length, 20.9 mm. Figure 61: CAS 064559; Isla Espíritu Santo, Baja California Sur; length, 19.5 mm.

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[2] DALL (1915:25, 26) also thought that some of Adams' types of *Semele* were mixed by the time Carpenter saw them and that *Amphidesma striosum* was such a case.

Type material and localities: *S. verrucosa*—UZM [no number], lectotype (KEEN, 1966b:12), pair; length, 10.6 mm; height, 8.0 mm; convexity, 3.3 mm (Figure 56). UZM, paralectotype, 1 pair. "Los Bocorones," Gulf of Nicoya, Puntarenas Prov., Costa Rica (approx. 9°50′N, 84°50′W), 37 m; A. S. Oersted, 1846–1848.

S. margarita—PRI 25935, holotype, right valve; length, 14.0 mm; height, 11.2 mm; convexity, 2.3 mm [pair would be 4.6 mm] (Figure 57). W side of Isla del Rey, Islas de las Perlas, Panama (approx. 8°20′N, 78°57′W).

Description: Small (to 23.7 mm; ANSP 225090; Venado Beach, Panama); oval; equivalve; shells average in thickness; longer, sharply rounded anteriorly; truncate posteriorly; antero-dorsal margin straight, with an elongate lunule and a flattened area adjacent to it; postero-dorsal margin straight, with an escutcheon. Periostracum thin, tan. Sculpture of heavy concentric ribs that sometimes are obsolete on posterior slope (if present, carinate along escutcheon); radial sculpture present at least on anterior ends of both valves (7 or 8 ribs); radial sculpture present on posterior slope of both valves in young specimens, sometimes persisting into adult, but more often obsolete; radial sculpture persisting over entire right valve in some specimens (as in type of *Semele margarita*), giving these specimens a cancellate appearance. Externally white, with tan or purple flecks or rays; beaks with a characteristic purple ray on anterior slope; white within, with purple rays showing through; hinge purple. Pallial sinuses large.

I have also illustrated a typical adult pair from Costa Rica (CAS 064536) (Figure 58).

Distribution and habitat: San Juan del Sur, Rivas Prov., Nicaragua (11°15′30″N, 85°53′W) (SDNHM 28857), to Isla Otoque, Islas Bonas (8°36′N, 79°39′W) (LACM 65-21), and Isla del Rey, Islas de las Perlas (8°20′N, 78°57′W) (type of *Semele margarita*; LACM 124444), Panama. Intertidal zone to 23 m (mean, 10 m), on sand. I have examined 23 lots.

CRUZ *et al.* (1980:90) report *Semele pacifica* (Dall) from Estero Salado, Guayas Prov., Ecuador (2°39′S, 80°9′W). Their record might have been based on this subspecies, but without being able to verify their material, I am unable to accept this record; it could have been based on a specimen *S. pulchra* (Sowerby) instead.

Remarks: Understanding the relationships within this species complex proved to be a most challenging problem. As additional material becomes available, my tentative conclusions may have to be modified.

Early interpretations of Mörch's *Semele verrucosa* were incorrect and based on misidentifications of *S. formosa* (Sowerby) (COAN, 1983). Only after one of Mörch's specimens was illustrated (KEEN, 1966b) was the correct interpretation possible.

Olsson's *Semele margarita* is a synonym of *S. verrucosa*. It is based on a small right valve that retains a lot of radial sculpture. Such right valves are not uncommon and, in fact, help to demonstrate the relationship of *S. verrucosa* to the more northerly *S. pacifica* Dall and to account for records of the latter in Panama. (In *S. v. pacifica,* the right valve almost always has abundant radial sculpture, whereas in the left valve the radial rays are confined to the anterior and posterior ends.)

In some adult specimens of *Semele verrucosa verrucosa,* the radial sculpture is confined to the anterior slope of both valves, being overridden on the central slope by concentric sculpture and disappearing on the posterior slope, which becomes flattened. Growth series, the young portions of adult specimens, and variation within lots reveal that only one taxon is present from southern Nicaragua to Panama.

A specimen with only traces of radial sculpture on the posterior slope accounts for Olsson's record of *Semele guaymasensis* from Panama. *Semele guaymasensis,* which has similarly restricted radial sculpture, is at present known only as far south as Jalisco, Mexico. It also has smoother beaks, has no radial sculpture on the posterior slope at any stage, and has concentric sculpture that continues onto the posterior slope, often forming a carina at the margin of the beveled escutcheon.

The tendency of *Semele verrucosa* to lose its radial sculpture—and its relationship to the more northerly *S. pacifica*—is further evidenced by some unusual specimens of the latter from Bahía Cholla, Sonora, Mexico (for example, CAS 064717), in which the radial sculpture is somewhat subdued on the central slope of the right valve; this valve almost always has strong radial sculpture throughout.

I have here interpreted the relationship of the two as subspecies, but it is difficult to know where to draw the line between them. (1) There is no material in collections between Oaxaca, Mexico, and southern Nicaragua. (2) The few lots in collections from southern Mexico are worn valves that are morphologically similar to the southern subspecies. (3) There is one valve labeled as having come from northern Costa Rica (LACM 124443; Puerto Parker) that is indistinguishable from *Semele verrucosa pacifica* from the Gulf of California, but it may be mislabeled.

I hypothesize that *Semele verrucosa verrucosa* is of comparatively recent origin, as explained under *S. v. pacifica* below. *Semele guaymasensis,* rather than *S. v. verrucosa,* is thus compared and may be the most closely related to *S. anteriocosta* Vokes from the Miocene of the western Atlantic.

Semele verrucosa pacifica Dall, 1915

(Figures 59–61)

Semele pacifica Dall, 1915: DALL, 1915:27; I. OLDROYD, 1925:180–181; pl. 3, fig. 5; BURCH, 1945a:17; 1945b: 17; HERTLEIN & STRONG, 1949:240, 245–246, 258; pl. 1, fig. 11; KEEN, 1958:198–199; fig. 489; OLSSON, 1961: 360, 368, 538; pl. 65, fig. 3; KEEN, 1971:251–252; fig.

637; pl. 8, fig. 6; COAN, 1973:325; BERNARD, 1983:26, 69; GEMMELL *et al.*, 1987:56.

Semele jaramija Pilsbry & Olsson, 1941: PILSBRY & OLSSON, 1941:70, 79; pl. 17, fig. 5; HERTLEIN & STRONG, 1949: 240, 244, 258; pl. 1, fig. 12; DURHAM, 1950:91, 169, 170; pl. 24, fig. 7; pl. 25, fig. 6; HOFFSTETTER, 1952: 40–41; fig. 8; KEEN, 1958:196–197; fig. 484; OLSSON, 1961:361, 538; pl. 65, fig. 2 [not in main text]; KEEN, 1971:251 [as a synonym of *S. pacifica*].

Semele hertleini Durham, 1950: DURHAM, 1950:90–91, 169, 170; pl. 24, fig. 6; pl. 25, fig. 7.

Type material and localities: *S. pacifica*—USNM 211728, holotype, a slightly deformed right valve; length, 18.2 mm; height, 14.5 mm; convexity, 3.1 mm [pair would be about 6.2 mm] (Figure 59). Off La Paz, Baja California Sur, *Albatross* stn. 2822 (24°16′N, 110°22′W), 38 m, gray sand; 30 April 1888.

S. jaramija—ANSP 13709, holotype, a broken left valve (not a right, as stated by PILSBRY & OLSSON, 1941); length, 20.9 mm; height, 15.5 mm; convexity, 3.0 mm [pair would be about 6.0 mm] (Figure 60). Punta Blanca, about 8.5 km S of Cabo San Lorenzo, Manabi Prov., Ecuador (1°7′30″S, 80°53′30″W); Canoa Formation, Pliocene; A. A. Olsson, 1936–1938.

S. hertleini—UCMP 30367/A.3548, holotype, right valve; length, 15.5 mm; height, 11.4 mm; convexity, 2.2 mm [pair would be about 4.4 mm] (not figured here). UCMP 30368/A.3582, paratype, right valve. Seacliffs at south-central end, Isla Coronados, Baja California Sur (26°6′N, 111°17′W); Pleistocene.

Description: Small (to 26.6 mm; LACM 69-22; near Puertecitos, Baja California Norte); differing from *Semele v. verrucosa* in having a more elongate outline, finer sculpture, radial sculpture that is present on posterior slope in adults and over the entire surface of right valve.

KEEN (1971:pl. 8, fig. 6) gave an external view of a living specimen. I have illustrated an adult pair from the southern Gulf of California (CAS 064559) (Figure 61).

Distribution and habitat: Northeastern end of Isla Cedros, Baja California Norte (28°20′25″N, 115°11′20″W) (LACM 71-152), along the Pacific coast of Baja California, into and throughout the Gulf of California, southward to Puerto Huatulco, Oaxaca (15°44′50″N, 96°8′W) (LACM 38-9). Intertidal zone to 128 m (mean, 28 m), on sand substrates (a few labels note mud). I have examined 131 lots.

DALL's (1915) record from "Catalina Island, California," was based on USNM 73921, which actually came from Isla Santa Catalina in the Gulf of California.

One valve indicated as coming from farther south (LACM 124443; Puerto Parker, Costa Rica) is so much like material from the Gulf of California and so unlike other material from Costa Rica, that it may have been mislabeled.

This species has been reported from the Pleistocene of the Burica Peninsula, Costa Rica/Panama (OLSSON, 1942: 162, as "*S. jaramija*"), but this could have been based on the typical subspecies. It is known from the Pliocene of Ecuador (type locality of *Semele jaramija*), and HOFFSTETTER (1952) reported a pair as a "subfossil" [?Pleistocene] at Santa Elena, Ecuador.

Remarks: The synonymy of this subspecies and *Semele hertleini* is obvious. DURHAM (1950) did not compare the two.

HERTLEIN & STRONG (1949) first reported *Semele jaramija* from the Recent fauna. Their material was based on left valves of *S. v. pacifica*, which have radial sculpture confined to the ends. Ironically, HOFFSTETTER (1952) noted the discrepant sculpture in his pair, but he reported this species as *S. jaramija* and did not connect it to *S. pacifica*. KEEN (1971) first took the step of synonymizing the two.

This subspecies must have occurred as far south as Ecuador in the Pliocene and possibly the Pleistocene (Hoffstetter's "subfossil"). It is thus probably older than *Semele v. verrucosa*. No Recent material is as yet known of this subspecies from farther south than Oaxaca, Mexico, with a separable subspecies occurring from Nicaragua to Panama. Its antiquity may also be evidenced by the fact that it is homologous to the western Atlantic *Semele bellestriata* (CONRAD, 1837:239–240; pl. 20, fig. 4), which occurs from the Miocene to the Recent (BOSS, 1972:20–23). The latter has heavier shells than *S. v. pacifica*, and has strong radial sculpture in both valves.

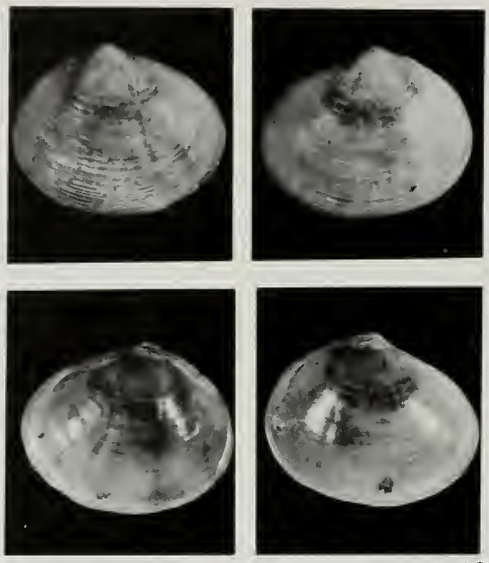
Semele, s.l., no group

Semele ***jamesi*** Coan, sp. nov.

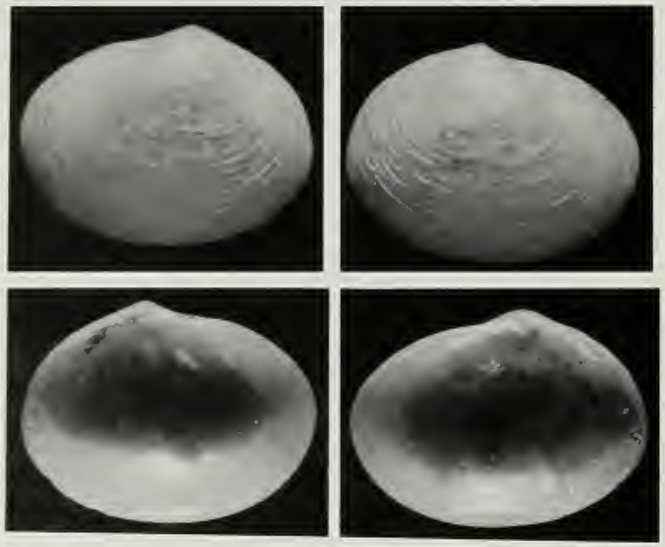
(Figures 62, 63)

Type material and locality: SBMNH 34941, holotype, pair; length, 5.4 mm; height, 4.35 mm; convexity, 2.3 mm (Figure 62). SBMNH 34942, paratypes, 28 pairs, 6 right valves, 1 left valve. (Some paratypes to be sent to AMNH, ANSP, BM(NH), SDNHM, and USNM, which lack any specimens of this species.) Bahía Chatham, Isla del Coco, Costa Rica (5°33′N, 87°2′30″W); 46–69 m, in coral rubble; Donald R. Shasky, Michel Montoya, and Kirstie Kaiser, 27 May 1985.

Description: Very small for genus (length to 7.3 mm; LACM 66-17; between El Tule and Palmilla, Baja California Sur); oval; equivalve; decidedly inflated; shells average in thickness for size; longer, sharply rounded anteriorly; broadly rounded to slightly truncate posteriorly; antero-dorsal margin with convex flare in young, straighter in adult, with a lunule; postero-dorsal margin slightly convex, with an escutcheon. Periostracum thin, light tan. Sculpture of thin, irregular, well-spaced concentric ribs, those near ventral margin with a frilly edge and often patchy, as if worn off in spots; also with fine radial ribs between concentric ribs. White externally and internally



62



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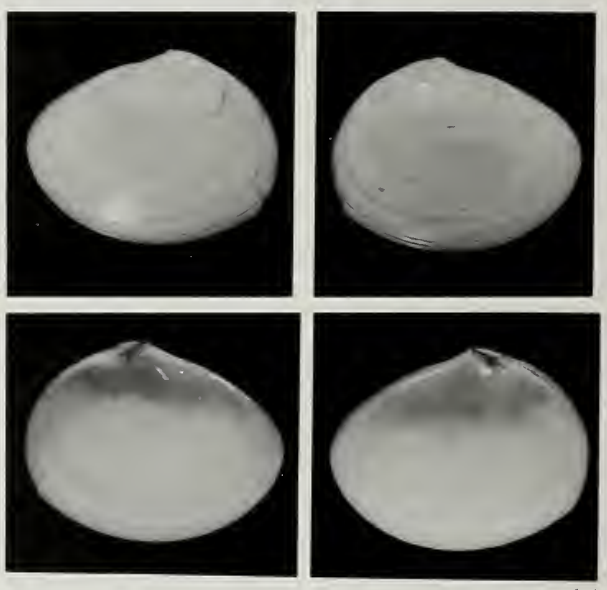

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Explanation of Figures 62 to 64

Figures 62 and 63. *Semele* ***jamesi*** Coan, sp. nov. Figure 62: Holotype; length, 5.4 mm. Figure 63: CAS 064566; Bahía San Carlos, Sonora, Mexico; length, 6.6 mm.

Figure 64. *Semele laevis* (Sowerby). Holotype of *Amphidesma laeve*; length, 36.4 mm.

in most, with radial brownish patches, particularly on anterior and posterior slopes. (Some specimens rosy or yellowish, some with brown radial bands.) Hinge not colored. Pallial sinuses large.

I have also illustrated a pair from Sonora, Mexico (CAS 064566) (Figure 63).

Comparisons: Shells of this species can most easily be distinguished by their small size. Juvenile shells of *Semele bicolor, S. lenticularis,* and *S. flavescens* are flatter and smoother, as is young *S. rosea.* Small *S. jovis* is also flatter, with more regular concentric sculpture. Close examination of the juveniles of *Semele* species that CARPENTER (1857c)

described as "*Tellina*" *lamellata* and "*T.*" *regularis* demonstrate that they are not small *S. jamesi*.

Distribution and habitat: Cabo San Lucas, Baja California Sur (22°52′N, 109°53′W) (LACM 66-12, 67-76), throughout the Gulf of California as far north as Puertecitos, Baja California Norte (30°20′N, 114°39′W) (LACM 64-31), and southward to Punta Mala, Manabi Prov., Ecuador (1°34′N, 80°50′W) (SBMNH 34929). It has been recorded from 5 to 161 m (mean, 38 m). This species apparently lives in sandy areas among rocks. I have examined 48 lots.

I suspect that this species may brood its young because of its small size. However, I opened a number of live-collected specimens and could detect no broods in the dried soft parts.

Remarks: This species is named for Dr. James H. McLean of the Los Angeles County Museum of Natural History.

Referred material:

Collection	Locality	Depth (m)
	Baja California Sur	
LACM 67-76	Cabo San Lucas	30
LACM 67-12	Cabo San Lucas	24–35
LACM 66-17	between El Tule & Pamilla	18–37
LACM 66-19	Cabo Pulmo	1.5–6
LACM 66-23	Punta Ventana	18–37
LACM 69-58	Isla Cerralvo	50–200
LACM 66-30	La Paz	37–55
CAS 064562	Isla Espíritu Santo	26–46
SBMNH 34927	Isla Ballaena	11–15
LACM 60-8	Isla Monserrate	46–161
SBMNH 34928	Isla Monserrate	73–146
LACM 78-118	Isla Danzante	23–24
UCMP A.3610	Isla Carmen	31
UCMP A.3613	Isla Carmen	161
CAS 064565	Isla Carmen	unknown
SBMNH 34925	Isla Carmen	16–18
	Baja California Norte	
LACM 75-9	Bahía de los Angeles	27
LACM 76-2	Bahía de los Angeles	18–22
LACM 64-31	Puertecitos	7–18
	Sonora	
SBMNH 34926	Bahía San Carlos	100
CAS 064566	Bahía San Carlos [figured]	8–23
LACM 64-36	Guaymas	18–37
LACM 77-13	Guaymas	100
LACM 68-13	Guaymas	17–26
CAS 064564	Guaymas	unknown
CAS 064561	Guaymas	49–79
	Central Mexico	
LACM 67-12	San Blas, Nayarit	23
LACM 65-16	Bahía Banderas, Jalisco	18–27
LACM 68-45	Cuastocomate, Jalisco	18–37
Skoglund Coll.	Bahía Santiago, Colima	30–61
	Costa Rica	
LACM 72-17	Bahía Salinas	1.5–8
LACM 72-19	Bahía Jobo	1.5–11
LACM 72-7	Bahía Santa Elena	1.2–11
LACM 72-8	Bahía Santa Elena	16–29
LACM 72-30	Punta Santa Elena	12–15
LACM 72-40	Bahía Brasilito	18
LACM 72-36	Bahía Huevos	37–42
Skoglund Coll.	Bahía Culebra	12–21
LACM 72-38	Bahía Portrero	8–12
LACM 72-58	Punta Quepos	9–23
LACM 72-64	Isla del Caño	12
SBMNH 34941/2	Isla del Coco [type lot]	46–49
	Panama	
LACM 65-25	Isla Taboga	9–27
CAS 064563	Isla Taboga	6–16
	Ecuador	
SBMNH 34930	Isla la Plata	30–46
SBMNH 34931	Isla la Plata	30–46
SBMNH 34932	Isla la Plata	30–37
SBMNH 34929	Punta Mala	20

Semele laevis (Sowerby, 1833)

(Figure 64)

Amphidesma laeve Sowerby, 1833: Sowerby, 1833a:8; pl. 18, fig. 6; Sowerby, 1833b:199; Reeve, 1841:68; pl. 48, fig. 6; Hanley, 1843:44; 6; pl. 12, fig. 10; 1856:341; Reeve, 1853:pl. 7, fig. 50; Hanley, 1857:pl. 3, fig. 33; Tryon, 1869:120 [*Semele*]; Dall, 1909:271; Lamy, 1913:354, footnote; Pilsbry & Olsson, 1941:70; Hertlein & Strong, 1949:240, 245; Keen, 1958:198–199; fig. 487; Olsson, 1961:359, 361–362, 537; pl. 64, fig. 6; Cauquoin, 1969:575–576; Keen, 1971:251–252; fig. 635; Bernard, 1983:46.

Semele laevis costaricensis Olsson, 1922: Olsson, 1922:258, 286; pl. 29, fig. 1 [as a "var."]; Hodson & Hodson, 1931:17, 62; pl. 8, fig. 5; Olsson, 1964:65–66, 216; pl. 9, fig. 9; Jung, 1969:397–398, 611; pl. 36, figs. 1, 2; Woodring, 1982:677; pl. 115, figs. 19, 20; pl. 117, fig. 20.

Type material and localities: *A. laeve*—BM(NH) 1986072, holotype, pair; length, 36.4 mm; height, 28.0 mm; convexity, 10.5 mm (Figure 64). "Xipixapi" [Jipijapa; just inland from Puerto de Cayo], Manabi Prov., Ecuador (1°20′S, 80°45′W), 18 m, sandy mud; H. Cuming, 1828–1830.

S. laevis costaricensis—PRI 21287, holotype, right valve; length, 72.0 mm; height, 65.5 mm; thickness, 8.0 mm [pair would be 16 mm] (not figured here). Hill 3, Río Banano, Limón Prov., Costa Rica (about 9°55′N, 83°10′W); lower Gatun Formation; middle Miocene.

Description: Large (to 89.0 mm; Skoglund Coll.; Playas, Guayas Prov., Ecuador; Woodring (1982) cites a specimen 91.5 mm long, but I have no idea where it is); ovate-elongate; equivalve; shells thin; longer, produced ante-

riorly; rounded, slightly truncate posteriorly; antero-dorsal margin almost straight, with a small, elongate lunule; postero-dorsal margin rounded, with a narrow escutcheon. Periostracum light tan. Smooth externally, with concentric growth lines only. White externally and internally. Pallial sinuses medium-sized.

Distribution and habitat: Guaymas, Sonora, Mexico (about 27°55′N, 110°53′W) (CAS 064560), to Zorritos, Tumbez Prov., Peru (3°40′S, 80°40′W) (Olsson, 1961). The most southerly station from which I have seen specimens is Playas, Guayas Prov., Ecuador (2°39′S, 80°23′W) (CAS 064673), but I see no reason to doubt Olsson's record. From the intertidal zone to 27 m (mean, 18 m), on sand and mud bottoms. I have seen 33 lots.

This species is recorded from Pleistocene strata on the Burica Peninsula, Costa Rica (Olsson, 1942:10), and the Santa Elena Peninsula, Ecuador (Hoffstetter, 1948: 80); from a Pliocene formation in Ecuador (Pilsbry & Olsson, 1941); and from middle Miocene strata in Costa Rica (Olsson, 1922), Panama (Woodring, 1982), Ecuador (Olsson, 1964), Peru (Olsson, 1932:126), Trinidad (Jung, 1969), and Venezuela (Hodson & Hodson, 1931).

Remarks: Externally, this *Semele* could be mistaken for a *Tellina* or a *Macoma,* but the internal ligament shows its true affinities.

Olsson's variety, *Semele laevis constaricensis,* was originally differentiated from *S. laevis* as being longer and more evenly rounded posteriorly. Later, Olsson (1964) described its antero-dorsal margin as being more elliptical, longer, straight, and downward sloping; and its anterior end as being more narrowly rounded. Jung (1969) said that it is smaller, with a narrower pallial sinus, and with shorter, thicker cardinal teeth in the right valve. Woodring (1982) also said that it is smaller.

The difference in maximum size seems to be of little significance—89.0 mm (perhaps 91.5 mm) for Recent material, 72 mm for Olsson's type, and 75 mm calculated by Woodring for one specimen from the Gatun Formation in Panama. Shell shape in Recent material is quite variable; insufficient material was available to earlier workers. The proportions are also variable in fossil material, as is well illustrated by Woodring (height-length from 0.68 to 0.87); and the shapes of the anterior and posterior ends also differ among specimens. Moreover, I do not see much difference in the shape of the pallial sinuses or the cardinal teeth between the specimen figured by Jung (1969) and Recent material.

Excluded Taxon

Semele mediamericana Pilsbry & Lowe (1932:92–93, 144; pl. 12, figs. 1, 1a, 2) was not described from material collected by Lowe as were most other species in that paper but from specimens in the ANSP collection (ANSP 53295), labeled "Nicaragua, McNeil." It subsequently appeared in other works on the eastern Pacific fauna (Hertlein & Strong, 1949; Keen, 1958). Contrary to published statements, this specimen was probably not mislabeled; it was merely from the Caribbean coast of Nicaragua. It is a synonym of *S. proficua* (Pulteney, 1799) (Boss, 1972:9, 11).

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LITERATURE CITED

All works cited in the text, including sources of taxonomic units, are listed. Volume, bulletin, monograph, memoir, and professional paper numbers are in bold face; series numbers, in parentheses, precede volume numbers; issue numbers, in parentheses, follow volume numbers; supple-

mentary information, such as second methods of listing volumes, part numbers, and parenthetical statements are given in brackets. Plates are listed, but not text figures, maps, charts, or tables. Exact publication dates are given when possible.

ADAMS, A. 1854. Descriptions of new species of *Semele, Rhizochilus, Plotia* and *Tiara* in the Cumingian collection. Zool. Soc. Lond., Proc. **for 1853**[pt. 21](153-154):94-99 (25 July).

ADAMS, A. & G. F. ANGAS. 1864. Descriptions of new species from the Australian seas, in the collection of Gense French Angas. Zool. Soc. Lond., Proc. **for 1863**(3):418-428; pl. 37 (April).

ADAMS, A. & L. A. REEVE. 1848-1850. Mollusca. x + 87 pp.; 24 pls. *In:* A. Adams (ed.), The zoology of the voyage of H.M.S. *Samarang,* under the command of Captain Sir Edward Belcher, . . . during the years 1843-1846. Reeve, Benham, & Reeve: London [pp. 1-24; ?pls. 1-9 (Nov. 1848); 25-44; ?pls. 10-13 (May 1850); pp. 45-87, i-x; ?pls. 14-24 (Aug. 1850)].

ADAMS, C. B. 1852a. Catalogue of shells collected at Panama, with notes on synonymy, station and habitat, ... Lyc. Natur. Hist. New York, Ann. **5**:229-296 (June); 297-549 (July).

ADAMS, C. B. 1852b. Catalogue of shells collected at Panama, with notes on their synonymy, station, and geographical distribution. Craighead: New York. viii + 334 pp. [a reprint of the above; concerning these works, see CARPENTER, 1864a; TURNER, 1956].

ADAMS, H. & A. ADAMS. 1856 [1853-1858]. The genera of Recent Mollusca; arranged according to their organization. van Voorst: London. **1**:xl + 484 pp.; **2**:661 pp.; **3**, Atlas:138 pls. [Vol. 2:408 (Nov. 1856)].

ADDICOTT, W. O. 1966. Late Pleistocene marine paleoecology and zoogeography in central California. U.S. Geol. Surv., Prof. Paper **523C**:21 pp.; 4 pls.

ADEGOKE, O. S. 1969. Stratigraphy and paleontology of the marine Neogene formations of the Coalinga region, California. Univ. Calif. Publ. Geol. Sci. **80**:269 pp.; 13 pls. (25 Sept.).

ARNOLD, R. 1903. The paleontology and stratigraphy of the marine Pliocene and Pleistocene of San Pedro, California. Calif. Acad. Sci., Mem. **3**:420 pp.; 37 pls. (27 June) [also issued simultaneously as Stanford Univ., Contrib. to Biol. from the Hopkins Seaside Lab., No. 31].

BARKER, R. W. 1933. Notes on the Tablazo faunas of S.W. Ecuador. Geol. Mag. **70**(824):84-90 (Feb.).

BERNARD, F. R. 1983. Catalogue of the living Bivalvia of the eastern Pacific Ocean: Bering Strait to Cape Horn. Canadian Spec. Publ. Fisheries & Aquatic Sci. **61**:viii + 102 pp. (15 April).

BOONE, L. 1928. Mollusks from the Gulf of California and the Perlas Islands. Yale Univ., Peabody Mus. Natur. Hist., Bingham Oceanogr. Coll., Bull. **2**(5):17 pp.; 3 pls. (Dec.).

BOSS, K. J. 1972. The genus *Semele* in the western Atlantic. Johnsonia **5**(49):32 pp.; 12 pls. (25 May).

BOSS, K. J. 1982. Mollusca. Pp. 945-1166. *In:* Sybil P. Parker (ed.), Synopsis and classification of living organisms. **1**. (McGraw-Hill: New York, New York. xviii + 1166 pp.; 87 pls.

BOSWORTH, T. O. 1922. Geology of the Tertiary and Quaternary periods in the north-west part of Peru, with an account of the palaeontology by Henry Woods, . . . , T. Wayland Vaughan, . . . , & J. A. Cushman, ... Macmillan: London. xxii + 434 pp.; 26 pls. (post-March).

BRANN, D. C. 1966. Illustrations to "Catalogue of the Collection of Mazatlan Shells" by Philip P. Carpenter. Paleo. Resh. Inst.: Ithaca, New York. 111 pp.; 60 pls. (1 April).

BRODERIP, W. J. & G. B. SOWERBY. (1st). 1832. [. . . the new species of Mollusca and Conchifera collected by Mr. Cuming, . . .] Zool. Soc. Lond., Proc. **for 1832**[pt. 2](17):50-61 (5 June).

BRUFF, S. C. 1946. The paleontology of the Pleistocene molluscan fauna of the Newport Bay area, California. Univ. Calif. Publ., Bull. Dept. Geol. Sci. **27**(6):213-240 (27 Feb.).

BRUGUIÈRE, J.-G., J. B. P. A. D. M. D. LAMARCK & J. B. G. M. BORY DE SAINT-VINCENT. 1791-1828. Tableau encyclopédique et méthodique des trois règnes de la nature. Vers, coquilles, mollusques, et polypiers. Agasse: Paris. viii + 180 + 16 pp.; 488 pls. [pls. 287-390 by Lamarck (pre-22 Sept. 1798)].

BURCH, J. Q. (ed.). 1945a. Family Semelidae. Pp. 16-19. *In:* Distributional list of the west American mollusks from San Diego, California to the Polar Sea. Part I: Pelecypoda. Conch. Club Southern California, Minutes **43**:43 pp. (Jan.).

BURCH, J. Q. (ed.). 1945b. Family Semelidae in index. P. 17. *In:* [same as above]. Conch. Club Southern California, Minutes **45**:21 pp. (March).

BURCH, J. Q. (ed.). 1945c. Additions and corrections. *In:* [same as above]. Conch. Club Southern California, Minutes **46**:30 (March).

CARPENTER, P. P. 1856. Description of new species of shells collected by Mr. T. Bridges in the Bay of Panama and its vicinity, in the collection of Hugh Cuming, Esq. Zool. Soc. Lond., Proc. **for 1856**[pt. 24](310):159-160; (311):161-166 (11 Nov.).

CARPENTER, P. P. 1857a. Monograph of the shells collected by T. Nuttall, Esq., on the Californian coast, in the years 1834-5. Zool. Soc. Lond., Proc. **for 1856**[pt. 24](314):209-224; (315):225-229 (26 Jan.).

CARPENTER, P. P. 1857b. Report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. British Assoc. Adv. Sci., Rept. **26**[**for 1856**]: 159-368 + 4 pp.; pls. 6-9 (pre-22 April).

CARPENTER, P. P. 1857c. Catalogue of the collection of Mazatlan shells, in the British Museum: collected by Frederick Reigen, ... British Museum: London. i-iv + ix-xvi + 552 pp. (1 Aug.) [Warrington ed., viii + xii + 552 pp., published simultaneously] [reprinted: Paleo. Resh. Inst., 1967].

CARPENTER, P. P. 1864a. Review of Prof. C. B. Adams's 'Catalogue of the Shells of Panama,' from the type specimens. Zool. Soc. Lond., Proc. **for 1863**(3):339-369 (April) [reprinted in CARPENTER, 1872:173-205].

CARPENTER, P. P. 1864b. Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Brit. Assoc. Adv. Sci., Rept. **33**[**for 1863**]:517-686 (post-1 Aug.) [reprinted in CARPENTER, 1872:1-172].

CARPENTER, P. P. 1864-1866. Description of new marine shells from the coast of California. Parts I-III. Calif. Acad. Sci., Proc. I:**3**:155-159 (July 1864); II:175-176 (Dec. 1864); 177 (Jan. 1865); III:207-208 (post-4 Sept. 1865); 209-224 (Feb. 1866).

CARPENTER, P. P. 1872. The mollusks of western North America. Embracing the second report made to the British Association on this subject, with other papers; reprinted by permission, with a general index. Smithsonian Inst. Misc. Colln. **10**(252):xii + 325 + 13-121 pp. (Dec.).

CAUQUOIN, M. 1969. Mollusques récoltés par M. R. Hoffstetter sur les côtes de l'Équateur et aux Iles Galapagos. Semelidae et Donacidae. Mus. Nation. d'Hist. Natur., Bull. (2)**40**(3):574-584 (31 Jan.).

CHACE, E. P. 1956. Additional notes on the Pliocene and Pleistocene fauna of the Turtle Bay area, Baja California, Mexico. San Diego Soc. Natur. Hist., Trans. **12**(9):177–180 (11 June).

CHILDREN, J. G. 1823 [1822–1823]. Lamarck's genera of shells. Quart. Jour. Sci. Lit. Arts (London) **14**(27):64–87; pls. 3, 4 (Oct. 1822); (28):298–322; pls. 5, 6 (Jan. 1823); **15**(29): 23–52; pls. 2, 3 (April 1823); (30):216–258; pls. 7, 8 (July 1823); **16**(31):49–79; pl. 5 (Oct. 1823); (32):241–264; pl. 6 ("Jan. 1824," but probably Dec. 1823) [concerning: KENNARD *et al.* (1931)].

CLARK, A. 1931. The cool-water Timms Point Pleistocene horizon at San Pedro, California. San Diego Soc. Natur. Hist., Trans. **7**(4):25–42 (19 Dec.).

COAN, E. V. 1973. The northwest American Semelidae. Veliger **15**(4):314–329; 2 pls. (1 April).

COAN, E. V. 1983. A *Semele* story (Bivalvia: Semelidae). Nautilus **97**(4):132–134 (28 Oct.).

CONRAD, T. A. 1837. Descriptions of new marine shells from Upper California, collected by Thomas Nuttall, Esq. Acad. Natur. Sci. Philadelphia, Jour. **7**(2):227–268; pls. 17–20 (21 Nov.) [concerning: CARPENTER (1857a), KEEN (1966a)].

CRUZ P., M., M. D. GONZALEZ, E. GUALANCANAY & F. VILLAMAR. 1980. Lista de la fauna sublitoral de Estero Salado Inferior, Ecuador. Acta Oceanogr. del Pacifico, INOCAR, Ecuador **1**(1):82–96 (Oct.).

DALL, W. H. 1871. Descriptions of sixty new forms of mollusks from the west coast of North America and the North Pacific Ocean, with notes on others already described. Amer. Jour. Conch. **7**(2):93–160; pls. 13–16 (2 Nov.).

DALL, W. H. 1892. Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River. Part II. Streptodont and other gastropods, concluded. Wagner Free Inst. Sci. Philadelphia, Trans. **3**(2):201–473; pls. 13–22 (Dec.).

DALL, W. H. 1900. . . . Part V. Teleodesmacea: *Solen* to *Diplodonta*. Wagner Free Inst. Sci. Philadelphia, Trans. **3**(5):949–1218; pls. 36–47 (Dec.).

DALL, W. H. 1909. Report on a collection of shells from Peru, with a summary of the littoral marine Mollusca of the Peruvian zoological province. U.S. Natl. Mus., Proc. **37**(1704): 147–294; pls. 20–28 (24 Nov.).

DALL, W. H. 1915. Notes on the Semelidae of the west coast of America, including some new species. Acad. Natur. Sci. Philadelphia, Proc. **67**:25–28 (2 March).

DALL, W. H. 1921. New shells from the Pliocene or early Pleistocene of San Quentin Bay, Lower California. West American Scientist **19**(3):21–23 (15 June).

DALL, W. H. 1925. Illustrations of unfigured types of shells in the collection of the United States National Museum. U.S. Natl. Mus., Proc. **66**(2554):1–41; pls. 1–36 (22 Sept.).

DANCE, S. P. 1986. A history of shell collecting. Brill: Leiden. xv + 265 pp.; 32 pls.

DARWIN, C. R. 1846. Geological observations on South America. Being the third part of the geology of the *Beagle* . . . during . . . 1832 to 1836. Smith, Elder & Co.: London. vii + 279 pp.; 5 pls. [reprinted in several editions].

DARWIN, C. R. 1962. The voyage of the *Beagle*. Anchor, Doubleday: Garden City, New York. xxxi + 524 pp.; 6 pls. [reprint of 1860 ed.].

DE GREGORIO, A. 1884. Studi su talune conchiglie Mediterranee viventi e fossili con una rivista del gen. *Vulsella*. Soc. Malac. Italiana, Bull. **10**:36–288; pls. 1–5.

DELONG, J. H. 1941. The paleontology and stratigraphy of the Pleistocene at Signal Hill, Long Beach, California. San Diego Soc. Natur. Hist., Trans. **9**(25):229–252 (30 April).

DESHAYES, G. P. 1850 [1839–1858]. Traité élémentaire de conchyliologie avec les applications de cette science à la géologie. V. Masson: Paris. **1**:xii + 368 + 824 pp.; **2**:384 pp.; Atlas:80 + xi pp.; 132 pls. [**1**(2):129–824 (1850)].

DOELLO-JURADO, M. 1949. Dos nuevas especies de bivalvos marinos. Mus. Hist. Natur. de Montevideo, Comun. Zool. **3**(57):8 pp.; 1 pl. (16 Nov.).

D'ORBIGNY, A. D. 1845 [1834–1847]. Voyage dans l'Amérique Méridionale . . . , exécuté pendant les années 1826 . . . . **5**(3) [Mollusques]. xliii + 758 pp.; 85 pls. (in Atlas) Bertrand: Paris and Levrault: Strasbourg [pp. 529–600 (1845)].

DRAPER, B. C. 1987. Lost operculum club list of champions—marine shells of the eastern Pacific Alaska to Chile. Conch. Club Southern Calif.: Los Angeles, California. 43 pp. (June).

DUNKER, W. 1882. Index molluscorum Maris Japonici. Fischer: Cassellis. vii + 301 pp.; 16 pls.

DURHAM, J. W. 1950. 1940 E. W. Scripps cruise to the Gulf of California. Pt. II: Megascopic paleontology and marine stratigraphy. Geol. Surv. Amer., Mem. **43**:viii + 216 pp.; 48 pls. (10 Aug.).

DUSHANE, H. 1962. A checklist of mollusks for Puertecitos, Baja California, Mexico. Veliger **5**(1):39–50 (1 July).

EMERSON, W. K. & L. G. HERTLEIN. 1964. Invertebrate megafossils of the Belvedere Expedition to the Gulf of California. San Diego Soc. Natur. Hist., Trans. **13**(7):333–368 (30 Dec.).

EMERSON, W. K., G. L. KENNEDY, J. F. WEHMILLER & E. KENNAN. 1981. Age relations and zoogeographic implications of late Pleistocene marine invertebrate faunas from Turtle Bay, Baja California Sur, Mexico. Nautilus **95**(3): 105–116 (10 July).

FINÉT, Y. 1985. Preliminary faunal list of the marine mollusks of the Galápagos Islands. Inst. Royal Sci. Natur. Belgique, Doc. de Travail **20**:50 pp. (pre-21 March).

FISCHER, P. 1857. Observations anatomiques sur des mollusques peu connus (suite). Jour. Conchyl. **6**[(2)**2**](4):327–339; pl. 13 (Dec.).

GARDNER, J. A. 1928. The molluscan fauna of the Alum Bluff group of Florida. Part V. Tellinacea, Solenacea, Mactracea, Myacea, Molluscoidea. U.S. Geol. Surv., Prof. Paper **142E**: 185–249 + iv + iii pp.; pls. 29–36 (5 June).

GAY, C. 1854, 1858. See HUPÉ, L. H. (1854, 1858).

GEMMELL, J., C. M. HERTZ & B. W. MYERS. 1980. Seastar predation on mollusks in the San Felipe Bay area, Baja California, Mexico. Festivus **12**(3):24–55 (March).

GEMMELL, J., B. W. MYERS & C. M. HERTZ. 1987. A faunal study of the bivalves of San Felipe and environs, Gulf of California, from the Gemmell collection (1965 to 1976). Festivus **18**(Suppl.):72 pp. (26 Feb.).

GIGOUX, E. E. 1935. Los moluscos marinos de Atacama. Rev. Chilena Hist. Natur. Pura y Aplicada **38**:274–286.

GMELIN, J. F. 1791. Caroli a Linné . . . Systema naturae per regna tria naturae . . . editio decima tertia, acuta, reformata 1(6). Beer: Leipzig. Pp. 3021–3910 (pre-14 May) [another printing: "Rudolphipoli" on last p., with some text differences].

GOULD, A. A. 1850. [. . . shells from the Exploring Expedition . . . described by Dr. Gould.] Boston Soc. Natur. Hist., Proc. **3**(3):214–218 (May).

GOULD, A. A. 1851. [Descriptions of a number of California shells, collected by Maj. William Rich and Lieut. Thomas P. Green, United States Navy, ...] Boston Soc. Natur. Hist., Proc. **4**(4):87–93 (Nov.).

GOULD, A. A. 1852–1860. Mollusca & shells. *In:* United States Exploring Expedition during the years 1838 . . . 1842. Under the command of Charles Wilkes, U.S.N. **12**:xv + 510 pp. ("1851," actually 15 Dec. 1852). Addenda et Corrigenda: *499–*510 (1856?). Atlas:16 pp.; 52 pls. ("1856," actually 15 Dec. 1860) Sherman: Philadelphia [private issue of text: Gould & Lincoln (Boston); private issue of Atlas: Sherman (Philadelphia), but with some differences in plate explanations].

GOULD, A. A. 1853. Descriptions of shells from the Gulf of California and the Pacific coasts of Mexico and California. Boston Jour. Natur. Hist. **6**(3):374–408; pls. 14–16 (Oct.).

GOULD, A. A. 1857. Catalogue of the Recent shells, with descriptions of the new species. *In:* Report on the Geology of the Route, U.S. Pacific Railroad Exploration Reports **5**(2), Appendix:330–336; pl. 11 [U.S. 33rd Cong., 2nd Sess., Senate Ex. Doc. 78, House Ex. Doc. 91] (post-6 April) [privately reprinted, 1858].

GOULD, A. A. 1862. Otia conchologia: descriptions of shells and mollusks from 1839 to 1862. Gould & Lincoln: Boston. iv + 256 pp.

GOULD, A. A. & P. P. CARPENTER. 1857. Descriptions of shells from the Gulf of California, and the Pacific coasts of Mexico and California. Part II. Zool. Soc. Lond., Proc. **for 1856**[pt. 24](313):198–208 (7 Jan.).

GRANT, U. S., IV & H. R. GALE. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions . . . . San Diego Soc. Natur. Hist., Mem. **1**:1036 pp.; 32 pls. (3 Nov.).

GRAUSTEIN, J. E. 1967. Thomas Nuttall, naturalist. Explorations in America, 1808–1841. Harvard Univ.: Cambridge, Massachusetts. xiv + 481 pp.

GRAY, J. E. 1828–1830. Spicilegia zoologica; or, Original figures and short systematic descriptions of new and unfigured animals. Treüttel, Würtz & Co.: London and Wood: Strand. **1**:1–8; pls. 1, 2, 5 [pls. 3, 4, 6 never issued, but photocopies of BM(NH) MS plates present in some sets] (1 July 1828); **2**:9–12; pls. 7–11 (Aug. 1830).

HANLEY, S. C. T. 1842–1856. An illustrated and descriptive catalogue of Recent bivalve shells. Williams & Norgate: London. xviii + 392 + 24 pp.; pls. 9–24 [pp. 1–32 (late 1842); pp. 1–32 reissue; 33–144; pls. 9–13; pl. expl. 1–8 (early 1843); 145–272 (late 1843); pls. 14–16; pl. expl. 9–12 (late 1844); pls. 17–19; pl. expl. 13–18 (1846); pls. 20–24; pl. expl. 19–24 (26 July 1855); i–xviii + 273–392 (1856)].

HANLEY, S. C. T. 1854–1858. The conchological miscellany. Williams & Norgate: London and Edinburgh. [11] pp.; 40 pls. (numbered by genus) [*Amphidesma* section issued 1 Oct. 1857].

HARTMAN, O. 1963. Submarine canyons of southern California. Part II. Biology. Allan Hancock Pacific Exped. **27**(2): 424 pp.

HEILPRIN, A. 1887. Explorations of the west coast of Florida and in the Okeechobee wilderness. Wagner Free Inst. Sci. Philadelphia, Trans. **1**:vii + 134 pp.; 19 + 2 pls. (May).

HERM, D. 1969. Marines Pliozän und Pleistozän in Nord- und Mittel-Chile unter besonderer Berücksichtigung der Entwicklung der Mollusken-Faunen. Zitteliana [Bayerischen Staatssammlung f. Paläo. und Hist. Geol., Abhandl.] **2**:159 pp.; 18 pls. (1 Sept.).

HERTLEIN, L. G. 1957. Pliocene and Pleistocene fossils from the southern portion of the Gulf of California. So. Calif. Acad. Sci., Bull. **56**(2):57–75; pl. 13 (31 Aug.).

HERTLEIN, L. G. & W. K. EMERSON. 1956. Marine Pleistocene invertebrates from near Puerto Peñasco, Sonora, Mexico. San Diego Soc. Natur. Hist., Trans. **12**(8):154–176; pl. 12 (7 June).

HERTLEIN, L. G. & U. S. GRANT, IV. 1972. The geology and paleontology of the marine Pliocene of San Diego, California. Part **2B**: Paleontology: Pelecypoda. San Diego Soc. Natur. Hist., Mem. **2**:135–409; frontis.; pls. 27–57 (21 July).

HERTLEIN, L. G. & A. M. STRONG. 1939. Marine Pleistocene mollusks from the Galapagos Islands. Calif. Acad. Sci., Proc. (4)**23**(24):367–380; pl. 32 (20 July).

HERTLEIN, L. G. & A. M. STRONG. 1949. Family Semelidae. Pp. 239–251; pl. 1. *In:* Eastern Pacific expeditions of the New York Zoological Soc. XLI. Mollusks from the west coast of Mexico and Central America. Part VIII. Zoologica **34**(4):239–258; pl. 1 (30 Dec.).

HERTLEIN, L. G. & A. M. STRONG. 1955a. Marine mollusks collected at the Galapagos Islands during the voyage of the *Velero III,* 1931–1932. Essays in the Natural Sciences in Honor of Captain Allan Hancock (Univ. Southern California Press):111–145; pl. A (26 July).

HERTLEIN, L. G. & A. M. STRONG. 1955b. Marine mollusks collected during the "Askoy" Expedition to Panama, Colombia, and Ecuador in 1941. Amer. Mus. Natur. Hist., Bull. **107**:159–318; pls. 1–3 (28 Nov.).

HERTZ, C. M. 1986. Herbert Nelson Lowe, 1880–1936. A gifted amateur conchologist from southern California. Festivus **18**(3):26–43 (13 March).

HODSON, F. & H. K. HODSON. 1931. Some Venezuelan mollusks. Bull. Amer. Paleo. **16**(59):1–94; 24 pls. (1 Oct.).

HOFFSTETTER, R. 1948. Notas sobre el Cuaternario de la Peninsula de Santa Elena (Ecuador). II. Pelecypoda del Tercer Tablazo. Quito, Bol. Inform. Cient. Nacion. **2**(13/14):67–83 (Dec.).

HOFFSTETTER, R. 1952. Moluscos subfósiles de los estanques de sal de Salinas (Pen. de Santa Elena, Ecuador). Comparación con la fauna actual del Ecuador. Quito, Inst. Cienc. Natur. **1**(1):3–79 (June).

HOLTEN, H. S. 1802. Enumeratio systematica conchyliorum beat. J. H. Chemnitz . . . quae publica auctione veduntur die . . . . Havniae (Scidelini). [vi] + 88 pp.

HUPÉ, L. H. 1854–1858. Moluscos. *In:* C. Gay (ed.), Historia fisica y politica de Chile, ... Fauna Chilena. Zoologia **8**: 499 pp. (1854); Atlas **2**:8 + 6 pls. (1858, as "1854").

JOHNSON, R. I. 1964. The Recent Mollusca of Augustus Addison Gould. U.S. Natl. Mus., Bull. **239**:182 pp.; 45 pls. (28 July).

JORDAN, E. K. 1929. Report on fossils from Coquimbo. Pp. 117–119. *In:* B. Willis (ed.), Earthquake conditions in Chile. Carnegie Inst. Washington, Publ. **382**:xi + 178 pp.; 75 pls.; frontis.

JORDAN, E. K. [with introduction by L. G. Hertlein]. 1936. The Pleistocene fauna of Magdalena Bay, Lower California. Stanford Univ., Dept. Geol., Contrib. **1**(4):103–173; pls. 17–19 (13 Nov.).

JUNG, P. 1969. Miocene and Pliocene mollusks from Trinidad. Bull. Amer. Paleo. **55**(247):289–657; pls. 13–60 (5 Feb.).

KANAKOFF, G. P. & W. K. EMERSON. 1959. Late Pleistocene invertebrates of the Newport Bay area, California. Los Angeles Co. Mus. Natur. Hist., Contrib. in Sci. **31**:47 pp. (14 Oct.).

KEEN, A. M. 1958. Sea shells of tropical west America; marine mollusks from Lower California to Colombia. 1st ed. Stanford Univ. Press: Stanford, California. xii + 624 pp.; 10 pls. (5 Dec.).

KEEN, A. M. 1966a. West American mollusk types at the

British Museum (Natural History), I. T. A. Conrad and the Nuttall collection. Veliger **8**(3):167–172 (1 Jan.).

KEEN, A. M. 1966b. Moerch's west Central American molluscan types with the proposal of a new name for a species of *Semele*. Calif. Acad. Sci., Occ. Paper **59**:33 pp. (30 June).

KEEN, A. M. 1968. West American mollusk types at the British Museum (Natural History), IV. Carpenter's Mazatlan collection. Veliger 10(4):389–439; pls. 55–59 (1 April).

KEEN, A. M. 1969. [Families Scrobiculariidae and Semelidae]. Pp. 635–637. *In:* L. R. Cox *et al.* (eds.), Part N [Bivalvia], Mollusca 6, Vol. **2**:491–952. *In:* R. C. Moore (ed.), Treatise on invertebrate paleontology. Geol. Soc. Amer. and Univ. Kansas: Lawrence, Kansas. (Nov.).

KEEN, A. M. 1971. Sea shells of tropical west America; marine mollusks from Baja California to Peru. 2nd ed. Stanford Univ. Press: Stanford, California. xiv + 1064 pp.; 22 pls. (1 Sept.).

KEEP, J. 1904. West American shells. Whitaker & Ray: San Francisco. 360 pp.; frontis. (post-11 July).

KEEP, J. 1910. West Coast shells (revised edition). Whittaker & Ray-Wiggin: San Francisco. 346 pp.; frontis.; 3 pls. (Dec.).

KEEP, J. & J. L. BAILY, JR. 1935. West Coast shells. Stanford Univ. Press: Stanford, California and Oxford Univ.: London. xii + 350 pp. (post-1 Feb.).

KELLOGG, J. L. 1915. Ciliary mechanisms of lamellibranchs. Jour. Morphol. **26**(4):625–701 (20 Dec.).

KENNARD, A. S., A. E. SALISBURY & B. B. WOODWARD. 1931. The types of Lamarck's genera of shells as selected by J. G. Children in 1823. Smithsonian Inst., Misc. Coll. **82**(17):40 pp. (11 July).

KEW, W. S. W. 1924. Geology and oil resources of a part of Los Angeles and Ventura counties, California. U.S. Geol. Surv., Bull. **753**:viii + 202 pp.; 17 pls.

KOCH, F. C. L. & W. B. R. H. DUNKER. 1837. Beiträge zur Kenntniss de Norddeutschen Oolithgebildes und dessen Versteinerungen. Oehme & Müller: Braunschweig. 64 pp.; 7 pls. (post-May).

LAMARCK, J. B. P. A. D. M. D. 1798. See BRUGUIÈRE *et al.* (1791–1798).

LAMARCK, J. B. P. A. D. M. D. 1818. Histoire naturelle des animaux sans vertèbres. Vol. **5**:612 pp. Verdière, Deterville, & Lamarck: Paris (25 July).

LAMY, E. 1908. Coquilles marines recueillies par M. le Dr. Neveu-Lemaire pendant la Mission de Créqui-Montfort et Senechal de la Grange dans l'Amérique de Sud (1903) [suite]. Mus. Natl. d'Hist. Natur., Bull. **14**(1):44–53.

LAMY, E. 1910. Mollusques marins recueillis par M. le Dr. Rivet à Payta (Perou). Mission Serv. Géogr. de l'Armée pour la Mesure d'un Arc de Méridien Équatorial. . . . **9** [Zool.] (3):C79–91. Gauthier-Villars: Paris.

LAMY, E. 1912. Notes synonymiques sur les *Amphidesma* de Lamarck. Mus. Natl. d'Hist. Natur. Paris, Bull. **18**(3):159–166 (post-March).

LAMY, E. 1913. Révision des Scrobiculariidae vivants du Muséum d'Histoire Naturelle de Paris. Jour. Conchyl. **61**[(4)**15**] (3):243–368; pl. 8 (25 March).

LINNAEUS, C. 1767. Systema naturae per regna tria naturae . . . editio duodecima, reformata **1**(2):533–1327. Salvius: Stockholm.

LISTER, M. 1687 [1685–1692]. Historiae conchyliorum, ... Lister: London. [(1), 1685; (2), 1686; (3), 1687; (Appendix to 3), 1688; (4), 1688; (Appendix to 4), 1692].

MARINCOVICH, L. 1973. Intertidal mollusks of Iquique, Chile. Los Angeles Co. Natur. Hist. Mus., Sci. Bull. **16**:49 pp. (20 Feb.).

MAURY, C. J. 1917. Santo Domingo type sections and fossils. Bull. Amer. Paleo. **5**(29)[I]:165–284 [1–120] (31 March); 285–416 [121–252]; pls. 1–39 (29 April); (30)[II]:iii + 417–459 [1–43] (29 May).

MAURY, C. J. 1925. A further contribution to the paleontology of Trinidad (Miocene horizons). Bull. Amer. Paleo. **10**(42): 153–403 [1–252]; pls. 1–42 (27 March).

MÖRCH, O. A. L. 1860 [1859–1861]. Beiträge zur Molluskenfauna Central-Amerika's. Malak. Blätter **6**(4):102–106 (Oct. 1859); **7**(2):66–96 (July 1860); (3):97–106 (Aug. 1860); (4):170–192 (Dec. 1860); (5):193–213 (Jan. 1861) [concerning: KEEN (1966b)].

MONTAGU, G. 1808. Supplement to Testacea Britannica. White: London and Woolmer: Exeter. v + 183 + [5] pp.; pls. 17–30 (post-1 Oct.).

MÜLLER, T. 1836. Synopsis novorum generum, specierum et varietatum testaceorum viventium anno 1834 promulgatorum. Nicolai: Berlin. xii + 256 pp.

NATLAND, M. L. 1957. Paleoecology of West Coast Tertiary sediments. Pp. 543–571; 5 pls. *In:* H. S. Ladd (ed.), Treatise on marine ecology and paleoecology. **2** [Paleoecology]. Geol. Soc. Amer., Mem. **67**(2):x + 1077 pp. (25 March).

NICKLÈS, M. 1955. Scaphopodes et lamellibranches récoltés dans l'ouest Africain. Atlantidae Rept. **3**:93–237.

NOMLAND, J. O. 1917. The Etchegoin Pliocene of middle California. Univ. Calif. Publ., Bull. Dept. Geol. 10(14):191–254; pls. 6–12 (19 April).

OLDROYD, I. S. 1924. Marine shells of Puget Sound and vicinity. Univ. Washington, Puget Sound Biol. Station, Publ. **4**:272 pp.; 49 pls. (March).

OLDROYD, I. S. 1925. The marine shells of the west coast of North America. 1 [Pelecypoda]. Stanford Univ. Publ., Univ. Ser., Geol. Sci. **1**(1):247 pp.; 57 pls. (Sept.) [reprinted: Stanford Univ., 1978].

OLDROYD, T. S. 1925. The fossils of the Lower San Pedro fauna of Nob Hill Cut, San Pedro, California. U.S. Natl. Mus., Proc. **65**(2535):1–39; 2 pls. (16 Jan.).

OLSSON, A. A. 1922. The Miocene of northern Costa Rica, with notes on its general stratigraphic significance. Bull. Amer. Paleo. **9**(39)[1]:1–168 (1 April); [2]:169–309; 32 pls. (21 June).

OLSSON, A. A. 1932. Contributions to the Tertiary paleontology of northern Peru: Part 5, the Peruvian Miocene. Bull. Amer. Paleo. **19**(68):272 pp.; 24 pls. (30 June).

OLSSON, A. A. 1942. Tertiary and Quaternary fossils from the Burica Peninsula of Panama and Costa Rica. Bull. Amer. Paleo. **27**(106):157–258 [5–106]; pls. 14–25 [1–12] (25 Dec.).

OLSSON, A. A. 1961. Mollusks of the tropical eastern Pacific particularly from the southern half of the Panamic-Pacific faunal province (Panama to Peru). Panamic-Pacific Pelecypoda. Paleo. Resh. Inst.: Ithaca, New York. 574 pp.; 86 pls. (10 March).

OLSSON, A. A. 1964. Neogene mollusks from northwestern Ecuador. Paleo. Resh. Inst.: Ithaca, New York. 256 pp.; 38 pls. (28 Oct.).

OSORIO R., C., J. ATRIA C. & S. MANN F. 1979. Moluscos marinos de importancia economica en Chile. Serv. Nacion. Pesca, Biol. Pesc. **11**:3–47 (Aug.).

PALMER, K. E. H. (V. W.). 1958. Type specimens of marine Mollusca described by P. P. Carpenter from the West Coast (San Diego to British Columbia). Geol. Soc. Amer., Mem. **76**:viii + 376 pp.; 35 pls. (8 Dec.).

PALMER, K. E. H. (V. W.). 1963. Type specimens of marine Mollusca described by P. P. Carpenter from the west coast of Mexico and Panama. Bull. Amer. Paleo. **46**(211):285–408; pls. 58–70 (22 Oct.).

PARKER, R. H. 1964a. Zoogeography and ecology of some

macro-invertebrates, particularly mollusks, in the Gulf of California and the continental slope off Mexico. Vidensk. Medd. fra Dansk Naturhist. Foren. Bd. **126**:178 pp.; 15 pls. (17 Feb.).

PARKER, R. H. 1964b. Zoogeography and ecology of macro-invertebrates of Gulf of California and continental slope of western Mexico. Amer. Assoc. Petrol. Geol., Mem. **3**:331–376; 10 pls.

PEÑA G., G. M. 1971. Zonas de distribution de los bivalvos marinos del Peru. Univ. La Molina, Anal. Cient. **9**(3/4): 127–138.

PHILIPPI, R. A. 1860. Reise durch die Wueste Atacama auf Befehl der Chilenischen Regierung im Sommer 1853–54 unternommen und beschreiben. Anton: Halle. x + 192 + 62 pp.; 27 pls. [published simultaneously in Spanish].

PILSBRY, H. A. & H. N. LOWE. 1932. West Mexican and Central American mollusks collected by H. N. Lowe, 1929–31. Acad. Natur. Sci. Philadelphia, Proc. **84**:33–144; 17 pls. (21 May).

PILSBRY, H. A. & A. A. OLSSON. 1941. A Pliocene fauna from western Ecuador. Acad. Natur. Sci. Philadelphia, Proc. **93**: 1–79; pls. 1–19 (9 Sept.).

PILSBRY, H. A. & E. G. VANATTA. 1902. Papers from the Hopkins Stanford Galápagos Expedition, 1898–1899. XIII. Marine Mollusca. Wash. Acad. Sci., Proc. **4**:549–560; pl. 35 (30 Sept.).

PULTENEY, R. 1799. Catalogues of the birds, shells, and some of the more rare plants of Dorsetshire. Nichols: London. 92 pp.; 1 port. (pre-2 July).

RANSON, G. 1959. Mollusques de la plaine cotière soulevée de Guadalupito, récoltés par M. Bernado Boit. Jour. Conchyl. **99**[(4)**52**](2):66–76 (15 May).

RÉCLUZ, C. A. 1845. Monographie de génère Ligule, *Ligula*. Soc. Cuvierienne (Paris), Rev. Zool. **8**(10):377–385 (Oct.); (11):407–417 (Nov.).

REEVE, L. A. 1841–1842. Conchologia systematica, or complete system of conchology: . . . . Longman, Brown, Green, & Longmans: London. **1**:vi + 195 pp.; 129 pls. (1841); **2**:337 pp.; pls. 130–300 (1842).

REEVE, L. A. 1853. Monograph of the genus *Amphidesma*. *In:* Conchologia Iconica; or, Illustrations of the shells of molluscous animals **8**:7 pls. [pls. 1–4 (Oct.); pls. 5–7 (Nov.)].

RÜEGG, W. 1957. Geologie zwischer Cañete-San Juan, 13°00′–15°24′ Südperu. Geol. Rundsch. **45**(3):775–858; pl. 18 (Jan.).

SACCO, F. 1901. I molluschi dei Terreni Terziarii del Piedmonte e della Liguria, pt. **29**:216 pp.; 29 pls. Clausen: Torino (June).

SAY, T. 1822. An account of some of the marine shells of the United States. Acad. Natur. Sci. Philadelphia, Jour. **2**:221–224 (June); 225–248 (July); 257–276 (Aug.); 302–320 (Sept.); 321–325 (Nov.).

SCHENCK, H. G. 1945. Geologic application of biometrical analysis of molluscan assemblages. Jour. Paleo. **19**(5):504–521; pls. 66, 67 (4 Oct.).

SCHRENCK, L. I. 1867. Mollusken der Amur-Landes und des Nordjapanischen Meeres. Reisen und Forschungen im Amur-Lande in den Jahren 1854–1856 im Auftrage der Kaiserl. Akad. Wissensch. zu St. Petersburg ausgeführt und in Verbindung mit mehreren Gelehrten herausgegeben. . . . **2** [Zool.](3):259–974; pls. 12–30 (post-Oct.).

SCHRÖDER, O. 1916. Beiträge zur Anatomie von *Amphidesma solidum*. Jenaische Zeitschr. f. Naturwissensch. **54**(1):101–132 (21 July).

SCHUMACHER, C. F. 1817. Essai d'un nouveau système des habitations de vers testacés. Schultz: Copenhagen. [iv] + 287 pp.; 22 pls. (post-1 March).

SMITH, E. A. 1885. Report on the Lamellibranchiata collected by *H. M. S. Challenger*, during the years 1873–76. Zoology **13**(35):341 pp.; 25 pls. (post-1 Oct.).

SMITH, E. A. 1890. Report on the marine molluscan fauna of the island of St. Helena. Zool. Soc. Lond., Proc. **for 1890**(2): 247–317; pls. 21–24 (1 Aug.).

SOOT-RYEN, T. 1932. The Norwegian Zoological Expedition to the Galapagos Islands 1925, conducted by Alf Wollebaek. II. Pelecypods from Floreana (Sancta Maria) Galapagos Islands. Oslow, Meddel. f. Zool. Mus. **27** [Saertrykk av Nyt Magazin for Naturvidenskaberne **70**]: 313–324; pls. 1, 2 (30 April).

SOOT-RYEN, T. 1959. Pelecypoda. Report of the Lund University Chile Expedition. 1948–49, No. 35. Lunds Universitets Arsskrift (n.s.) (2)**55**(6):86 pp.; 4 pls. (18 Feb.).

SOWERBY, G. B. (1st). 18??. Species conchyliorum. Sowerby: London. [This work was cited by SOWERBY (1833a) and others, but it was never actually published. A few proof copies were distributed, and these, or photocopies of them, are in a number of libraries. In these, the numbers on the plates do not match the published citations. The plates on *Amphidesma* were later published by HANLEY (1857), with his own plate explanations.]

SOWERBY, G. B. (1st). 1832. See BRODERIP & SOWERBY (1832).

SOWERBY, G. B. (1st). 1833a. A catalogue of the Recent species of the genus *Amphidesma*. Pp. 1–2 [7–8 in 1841 reissue]; pls. 17–19. *In:* G. B. Sowerby, 2nd, Conchological illustrations: . . . . Sowerby: London. [iv + 116 pp.]; 200 pls. in 200 parts. Text for each genus paginated separately, and most also reissued in 1841. [*Amphidesma*—all no later than 8 March; most likely dates: pl. 17 (8 Feb. 1833); pl. 18 (15 Feb.); pl. 19, with first issue of text (22 Feb.).]

SOWERBY, G. B. (1st). 1833b. Characters of new species of Mollusca and Conchifera, collected by Hugh Cuming. Zool. Soc. Lond., Proc. **for 1832**[pt. 2](25):194–202 (13 March).

SPENGLER, L. 1798. Over det toskallede slaegt Tellinerne. Copenhagen, Skriv. Naturhist. Selsk. **4**(2):67–127; pl. 12.

STANLEY, S. M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). Geol. Soc. Amer., Mem. **125**: xiii + 296 pp.; 40 pls.

STEARNS, R. E. C. 1891. List of shells collected on the west coast of South America, principally between the latitudes of 7°30′S. and 8°49′N., by Dr. W. H. Jones, Surgeon, U.S. Navy. U.S. Natl. Mus., Proc. **14**(854):307–335 (20 Aug.).

STEARNS, R. E. C. 1894. The shells of the Tres Marias and other localities along the shores of Lower California and the Gulf of California. U.S. Natl. Mus., Proc. **17**(996):139–204 (19 July).

STOLICZKA, F. 1870 [1870–1871]. Cretaceous fauna of southern India **3**: The Pelecypoda, with a review of all known genera of this class, fossil and Recent, ... Geol. Surv. India, Mem., Palaeontologia Indica. xxii + 538 pp.; 50 + 4 pls. [pp. 1–222; pls. 1–12 (1 Sept. 1870); 223–409; pls. 13–28 (1 March 1871); xxii + 409–538; pls. 29–50 (1 Aug. 1871)].

STRONG, A. M. & L. G. HERTLEIN. 1939. Marine mollusks from Panama collected by the Allan Hancock Pacific Expedition to the Galapagos Islands, 1931–1932. Allan Hancock Pacific Expeditions **2**(12):177–245; pls. 18–23 (21 Aug.).

TAYLOR, J. D., W. J. KENNEDY & A. HALL. 1973. The shell structure and mineralogy of the Bivalvia. II. Lucinacea—Clavagellacea, conclusions. British Museum (Natur. Hist.), Bull. **22**(9):253–294; 15 pls. (16 March).

TOMLIN, J. R. L. B. 1927–28. The Mollusca of the 'St. George' Expedition. I. The Pacific coast of S. America. Jour. Conch. **18**(6):153–170 (Dec. 1927); (7):187–198 (May 1928).

TRYON, G. W., JR. 1869. Catalogue of the family Tellinidae.

In: Catalogue and synonymy of the genera, species and varieties of Recent Mollusca, described prior to January 1st, 1867, with dates of publication, references to plates, and localities. Pt. 2. Amer. Jour. Conch. **4**(5)[App.]:72–126 (6 May).

TURNER, R. D. 1956. The eastern Pacific marine mollusks described by C. B. Adams. Harvard Univ., Mus. Comp. Zool., Occ. Papers on Mollusks **2**(20):21–135; pls. 5–21 (22 Sept.).

TYLER, D. B. 1968. The Wilkes Expedition. The First United States Exploring Expedition (1838–1842). Amer. Philos. Soc.: Philadelphia. xvi + 435 pp.

VALENTINE, J. W. 1958. Late Pleistocene megafauna of Cayucos, California, with its zoogeographic significance. Jour. Paleo. **32**(4):687–696 (22 July).

VALENTINE, J. W. & J. H. LIPPS. 1963. Late Cenozoic rocky-shore assemblages from Anacapa Island, California. Jour. Paleo. **37**(6):1292–1302 (14 Dec.).

VALENTINE, J. W. & R. F. MEADE. 1961. Californian Pleistocene paleotemperatures. Univ. Calif. Publ. Geol. Sci. **40**(1): 1–46 (14 July).

VERRILL, A. E. 1870. Descriptions of shells from the Gulf of California. Amer. Jour. Sci. (2)**49**(146):217–227 (March).

VOKES, H. E. 1938. Upper Miocene Mollusca from Springvale, Trinidad, British West Indies. Amer. Mus. Novitates **988**: 28 pp. (16 May).

VOKES, H. E. & E. H. VOKES. 1962. Pelecypods from Barra de Navidad, Mexico. Nautilus **76**(2):61–63 (14 Nov.).

WEBB, R. W. 1937. Paleontology of the Pleistocene of Point Loma, San Diego County, California. San Diego Soc. Natur. Hist., Trans. **8**(24):337–348 (15 June).

WILLETT, G. 1946. Additional notes on the Pliocene molluscan fauna of Los Angeles City. So. Calif. Acad. Sci., Bull. **45**(1): 28–32 (10 June).

WILLIAMSON, M. B. 1892. An annotated list of the shells of San Pedro Bay and vicinity (With a description of two new species by W. H. Dall). U.S. Natl. Mus., Proc. **15**(898): 179–220; pls. 19–23 (2 Aug.).

WOOD, W. 1815. General conchology; or, A description of shells, arranged according to the Linnean system, ... **1.** Booth: London. lxi + 7 + 246 pp.; 59 + 1 pls.

WOODRING, W. P. 1982. Geology and paleontology of Canal Zone and adjoining parts of Panama. Description of Tertiary mollusks (Pelecypods: Propeamussiidae to Cuspidariidae; additions to families covered in P306-E; additions to gastropods; cephalopods). U.S. Geol. Surv., Prof. Paper **306F**: iv + 541–759; pls. 83–124 (about Sept.).

WOODRING, W. P. & M. N. BRAMLETTE. 1951. Geology and paleontology of the Santa Maria District, California. U.S. Geol. Surv., Prof. Paper **222**:iv + 185 pp.; 23 pls. [as "1950"].

WOODRING, W. P., R. B. STEWART & R. W. RICHARDS. 1941. Geology of the Kettleman Hills oil field, California: stratigraphy, paleontology, and structure. U.S. Geol. Surv., Prof. Paper **195**:v + 170 pp.; 57 pls. (7 June).

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A New Genus and Species of Prosobranch Gastropod (?Fasciolariidae) from the Mariana Islands

by

WILLIAM K. EMERSON

Department of Invertebrates, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, U.S.A.

AND

ROBERT B. MOFFITT

National Marine Fisheries Service, Southwest Fisheries Center Honolulu Laboratory, 2570 Dole Street, Honolulu, Hawaii 96822, U.S.A.

Abstract. A new genus and species of prosobranch gastropod, ***Falsilatirus pacificus,*** is described from deep water off Arakane Reef, in the Northern Mariana Islands. The questionable placement of this new species in the family Fasciolariidae is based on shell characters owing to the unavailability of soft parts for study.

INTRODUCTION

Deepwater shrimp trapping operations were conducted from 1982 to 1984 by the National Marine Fisheries Service, Southwest Fisheries Center Honolulu Laboratory as part of their Resource Assessment Investigation of the Mariana Archipelago (RAIOMA) program. Incidental catches in these operations included shells of several gastropod mollusks (D. B. Smith and R. B. Moffitt, unpublished data). Some of these mollusks were collected alive, but most were carried into baited traps by hermit crabs of the genus *Trizopagurus.* Among these transported shells were three crabbed specimens of a distinctive new genus and species of prosobranch gastropod that is described herein as ***Falsilatirus pacificus*** and tentatively placed in the Fasciolariidae.

SYSTEMATIC ACCOUNT

Family Fasciolariidae Gray, 1847

Falsilatirus Emerson & Moffitt, gen. nov.

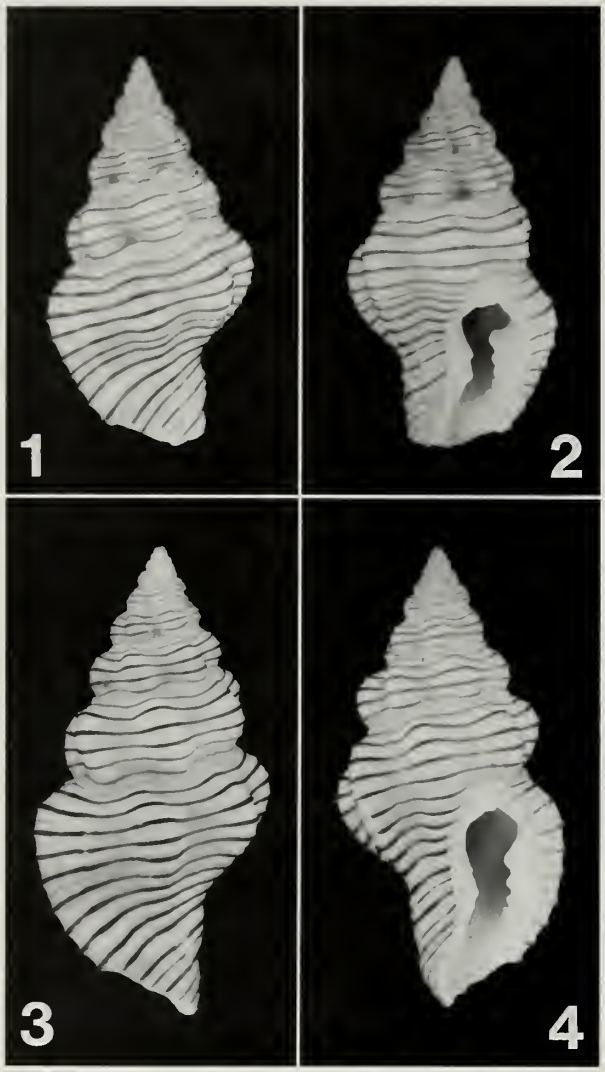
Type species: ***Falsilatirus pacificus*** Emerson & Moffitt, sp. nov.

Diagnosis: Shell in general shape and coloration somewhat resembles certain of the finely lirate *Latirus* Montfort, 1810, type species: *L. gibbulus* (Gmelin, 1791). Differs from the known fasciolariid genera in having distinctive labial and columellar dentition and by having a recurved siphonal canal. See description of the type species.

Falsilatirus pacificus Emerson & Moffitt, sp. nov.

(Figures 1–4)

Description: Shell angulate fusiform, solid and attaining 7½ postnuclear whorls (embryonic whorls not preserved) and 42+ mm in length. Post-embryonic whorls strongly axially ribbed, with 5 elongate nodules on the body whorl. Surface colored pale buff and ornamented with conspicuous, dark brown, evenly spaced spiral cords throughout. Midportion of whorls encircled with a paler, whitish band. Whorls of the spire with 3 or 4 dark brown, primary spiral cords; body whorl with 12 primary cords, extending from the suture to near the base. Interspaces between the primary spiral cords sculptured with a minor pale brown cord medially placed between 3 or 4 spiral lirations. Aperture white, prominently dentate with an open anal groove and a recurved siphonal canal (anterior portion lost to breakage). Outer lip with a submarginal, shelflike projection armed with 6 semifused denticles, the largest positioned posteriorly. Columella with a slightly raised outer margin



Explanation of Figures 1 to 4

Figures 1–4. Type specimens of ***Falsilatirus pacificus*** Emerson & Moffitt, sp. nov. Figures 1, 2: paratype a. Figures 3, 4: holotype. All figures ×1.5.

and with 2 denticle-like plicae, the anterior one forming a major fold. Radula and soft parts not seen.

Measurements in mm, holotype: 41.67 in length, 20.84 in width (Figures 3, 4); paratype a: 35.86 in length, 19.32 in width (Figures 1, 2); paratype b: 31.25 in length, 16.26 in width.

Type locality: Off Arakane Reef, Northern Mariana Islands, 15°38.4′N, 142°46.2′E, in 123–503 m (67–275 fathoms), NOAA ship *Townsend Cromwell,* cruise TC 83-05, station 167, taken in shrimp traps, 19 December 1983.

Distribution: Known only from the type locality.

Type depository: Holotype, American Museum of Natural History (AMNH), no. 225996; paratype a, United States National Museum, no. 859320; paratype b, AMNH no. 225997.

Remarks: As mentioned above, these specimens, which lack preserved embryonic whorls, suggest the fasciolariid genus *Latirus,* especially from the dorsal aspect and by the presence of a prominent spiral columellar fold. For example, see *Latirus angulatus* (Röding, 1798:118; Bullock, 1974:figs. 16–21) from the western Atlantic and *L. filosus* (Schubert & Wagner, 1829:100, pl. 227, figs. 4019, 4020; Abbott & Dance, 1982:184, illus.) from west Africa. The known latiroid species, however, have a nonrecurved siphonal canal and mostly lack denticles inside the outer lip. In the buccinid subfamily Pisaniinae Gray, 1857, many taxa possess shells with denticulate outer lips (subfamily reviewed by Cernohorsky, 1971, 1975), but generally lack a spiral ridge on the parietal wall. See especially *Clivipollia pulchra* (Reeve, 1846, *Ricinula,* no. 20, pl. 3, figs. 20a, b; Ponder, 1972:264, pl. 25, fig. 4; Abbott & Dance, 1982:172, illus.) from the western Pacific. On the bases of shell characters alone, data are not sufficient for unequivocal assignment to either the Fasciolariidae or Buccinidae. We have tentatively referred this new genus and species to the former family, owing largely to the presence of a distinctive columellar fold. Final familial placement must await the acquisition and study of the radula and soft parts of this new taxon.

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LITERATURE CITED

Abbott, R. T. & S. P. Dance. 1982. Compendium of seashells. E. P. Dutton, Inc.: New York. 411 pp.

Bullock, R. C. 1974. A contribution to the systematics of some West Indian *Latirus* (Gastropoda: Fasciolariidae). Nautilus 88(3):69–79.

Cernohorsky, W. O. 1971. Indo-Pacific Pisaniinae (Mollusca: Gastropoda) and related buccinid genera. Rec. Auckland Institute & Museum 8:137–167.

Cernohorsky, W. O. 1975. Supplementary notes on the taxonomy of buccinid species of the subfamily Pisaniinae (Mollusca: Gastropoda). Rec. Auckland Institute & Museum 12: 175–211.

Gray, J. E. 1847. A list of the genera of Recent Mollusca, their synonyma and types. Proc. Zool. Soc. Lond., for 1847: part 15, nos. 178–179, pp. 129–219.

Gray, J. E. 1857. Guide to the systematic distribution of Mol-

lusca in the British Museum. Part 1. London. i–xii + 230 pp.

MONFORT, P. D. DE. 1810. Conchyliologie systématique et classification méthodique des coquilles. . . . Paris. Vol. 2:676 pp.

PONDER, W. F. 1972. Notes on some species and genera of the family Buccinidae (Neogastropoda). Jour. Malacol. Soc. Australia 2(3):249–265.

REEVE, L. 1846. Conchologia Iconica: illustrations of the shells of molluscous animals. Monograph of the genus *Ricinula*. London. Vol. 3, text and 6 pls.

RÖDING, P. F. 1798. Museum Boltenianum . . . : pars secunda continens Conchylia. . . . J. C. Trappii: Hamburg. Pp. i–viii + 199.

SCHUBERT, G. M. & J. A. WAGNER. 1829. Systematisches Conchylien-Cabinet von Martini und Chemnitz, neu herausgegeben. . . . Nürnberg. Vol. 12, *Turbinella*, pp. 98–104, pl. 227.

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A Review of the Genus *Berthella* (Opisthobranchia: Notaspidea) from the Pacific Coast of North America

by

TERRENCE M. GOSLINER AND HANS BERTSCH

Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.

Abstract. Examination of specimens of *Berthella* from the Gulf of California and the Pacific coast of Baja California indicated morphological similarities with *B. stellata, B. pellucida,* and *B. tupala.* A detailed morphological review of specimens from the Mediterranean, Caribbean, Pacific, and Indian oceans revealed that all these taxa constitute a single, circumtropical species, *B. stellata.*

Specimens of *Berthella agassizii,* known previously only from the Caribbean and Brazil, are recorded from the Gulf of California and the Pacific coast of Baja California.

The morphology and systematics of three other species of *Berthella* from the northeastern Pacific are reviewed. The reproductive morphology of *B. californica* differs significantly from its original description. *Berthella kaniae* is regarded as a synonym of *B. martensi. Berthella strongi* was originally described as a *Pleurobranchus,* but all morphological features are consistent with *Berthella.* The genus *Pleurehdera* closely resembles *Berthella,* particularly in light of species examined in this study. Further study is required to assess its systematic position.

INTRODUCTION

Three species of the pleurobranchid genus *Berthella* Blainville, 1825, are currently known from the Pacific coast of North America. BERGH (1898) recorded *Berthella sideralis* (Lovén, 1847) from Unalaska. MACFARLAND (1966) stated that this record is dubious, in light of the fact that the buccal mass was absent from the mutilated specimen. No diagnostic characters that verify the identification were present. Therefore, there is no basis for considering this species as a member of the northeastern Pacific marine fauna. *Berthella californica* (Dall, 1900) was described from southern California. SPHON (1972) described *B. kaniae* from the Pacific coast of Mexico and Panama. Other specific and subspecific taxa have been erected in the genera *Berthella* and *Pleurobranchus,* such as *P. strongi* MacFarland, 1966, and will be discussed within this paper.

During 1984 and 1985 the California Academy of Sciences, the Centro de Investigaciones Científica y de Educación Superior de Ensenada, and Escuela Superior de Ciencias Marinas of the Universidad Autónoma de Baja California conducted three expeditions to Baja California. During these expeditions numerous opisthobranch specimens were collected. Included in these collections were specimens of two species of *Berthella.* One of these species resembles *B. stellata* (Risso, 1826), *B. pellucida* (Pease, 1860) and *B. tupala* Marcus, 1957. Two specimens, resembling the described morphology of *Berthella agassizii* (MacFarland, 1909), were collected from both coasts of Baja California. While comparing specimens of these taxa to other congeners, it was noted that several erroneous or incomplete descriptions had appeared in the literature. It therefore became necessary to review the members of the genus from the Pacific coast of North America, and to compare them to closely allied taxa in other temperate and tropical portions of the world.

DESCRIPTIONS

Berthella californica (Dall, 1900)

(Figures 1A, 2, 3)

Pleurobranchus californicus DALL, 1900:92.
Pleurobranchus chacei Burch, 1944: MACFARLAND, 1966:84.
Pleurobranchus californicus denticulatus MACFARLAND, 1966: 84, pl. 5, figs. 1–5, pl. 13, figs. 25–34, pl. 16, fig. 12.

Berthella californica (MacFarland, 1966): Lance, 1966:71.
Berthella denticulatus (MacFarland, 1966): Lee & Foster, 1985:442.

Distribution: Point Craven, Alaska to Point Loma, San Diego County, California (Behrens, 1980; Lee & Foster, 1985).

Material: One specimen, California Academy of Sciences, San Francisco, CASIZ 064823, Point Pinos, Monterey, 36°38′N, 121°56′W, F. M. MacFarland. One specimen, intertidal zone, Duxbury Reef, Bolinas, Marin County, California (37°53′N, 122°42′W), June 1968, T. M. Gosliner. One specimen, CASIZ 064824, intertidal zone, Point Pinos, Pacific Grove, Monterey County, California, June 1947, F. Pitelka.

External morphology: The color of the living specimen from Duxbury Reef closely resembles that depicted by MacFarland (1966) and Behrens (1980). The body is translucent white with numerous, scattered opaque white spots and marginal notal band (Figure 1A). The ctenidium is simply plicate without tubercles along the rachis.

Internal morphology: The calcified portion of the shell was completely dissolved in the specimens we examined. Its structure has been well documented by MacFarland (1966).

The jaws are armed with numerous elements bearing 0–4 denticles on either side of the prominent central cusp (Figure 2A). The radular formula in two specimens was 63 × 63·0·63 and 95 × 75·0·75. The inner lateral teeth (Figure 2B) are simple, hook-shaped, without basal denticles. Towards the outer margin of the radula, the teeth are more elongate (Figures 2C, D).

The reproductive system (Figure 3) was well developed in the fully mature specimen from Monterey. The description of its morphology is based primarily on the dissection of that specimen. The ampulla is thick and muscular. Proximally, it narrows into the postampullary duct, where it divides into the oviduct and vas deferens. The oviduct is short and enters the female gland mass. Adjacent to the ampulla, but not connecting with it, is the pyriform receptaculum seminis. From its proximal end a narrow duct curves distally and joins the vaginal duct near its juncture with the large, spherical bursa copulatrix. The vaginal duct is thick and convoluted. It exits at the genital atrium. The nidamental glands are well developed, but could not be differentiated, owing to poor preservation of that part of the reproductive system. The glands open into the genital atrium. From the division of the postampullary duct the vas deferens expands into a thick, convoluted prostatic portion. A simple penial gland enters the proximal end of the prostatic vas deferens. More proximally the vas deferens narrows into a muscular ejaculatory segment, consisting of numerous convolutions. From the proximal end of the vas deferens a large muscular penis emerges.

Discussion: MacFarland (1966) described *Pleurobranchus californicus denticulatus* as a distinct subspecies, based on the fact that specimens possess denticles on the jaw platelets. Both *P. californicus* and *P. californicus denticulatus* were transferred to *Berthella* (Roller, 1970), since they lack prominent tubercles on the rachis of the ctenidium. Most recent workers (Behrens, 1980; Willan, 1984) have considered *B. californica denticulata* as a synonym of *B. californica*. The fact that in the present material the jaw elements may or may not have denticles, even within different portions of the jaw of a single specimen, further supports this view. Furthermore, there is no geographical separation of specimens with and without denticles.

MacFarland (1966:pl. 16, fig. 12) described the reproductive anatomy of *Berthella californica denticulata*. He depicted a system without a receptaculum seminis and with the bursa copulatrix connecting directly to the oviduct. Examination of material in this study revealed that a receptaculum seminis is indeed present. Also, the oviduct enters the female gland mass near the albumen gland, rather than joining with the bursa copulatrix. The configuration observed in the present material is consistent with that found in other species of *Berthella*.

Berthella martensi (Pilsbry, 1896)

(Figures 1B, C, 4–6)

Pleurobranchus scutatus Martens in Möbius, 1880:309, pl. 21, fig. 8 (*non* Forbes, 1844).
Bouvieria scutata (Martens in Möbius, 1880): Vayssière, 1896:123, pl. 5, figs. 16–18.
Gymnotoplax martensi Pilsbry, 1896:211, pl. 48, figs. 34, 35.
Berthella martensi (Pilsbry, 1896): Willan, 1984, figs. 8–12, 21–28, 30–32, 40–42, 44.
Berthella kaniae Sphon, 1972:53, figs. 1–9; syn. nov.

Distribution: This species is known in the Indo-Pacific tropics from Mauritius, Western Australia, eastern Australia, Fiji, Enewetak, and Hawaii (Willan, 1984) and from the eastern Pacific from Baja California Sur to Panama (present study).

Material: Two specimens, Los Angeles County Museum, AHR 454-35, tidal flats, Secas Islands, Panama (7°57′N, 82°00′45″W), 6 Feb. 1935, Allan Hancock Foundation. One specimen, 7 m depth, Las Arenas, Gulf of California, Baja California Sur, Mexico (24°02′N, 109°49′W), 16 June 1985, H. Bertsch. Two specimens, CASIZ 064828, 20 m depth, Bomber Reef, Madang, Papua New Guinea (5°15′S, 145°45′E), 27 Oct. 1986, J. Darr. One specimen, CASIZ 064829, 30 m depth, northern pass, Madang, Papua New Guinea, 2 October 1986, T. Frohm.

External morphology: The living animals reach 50 mm in length. They exhibit considerable variation in coloration. In the Mexican and Panamanian specimens, the ground color was off-white with scattered light brown spots (Figure 1B). This color pattern closely resembles that shown by Willan (1984:fig. 21) for a specimen from Enewetak. Two of the specimens collected from Papua New Guinea

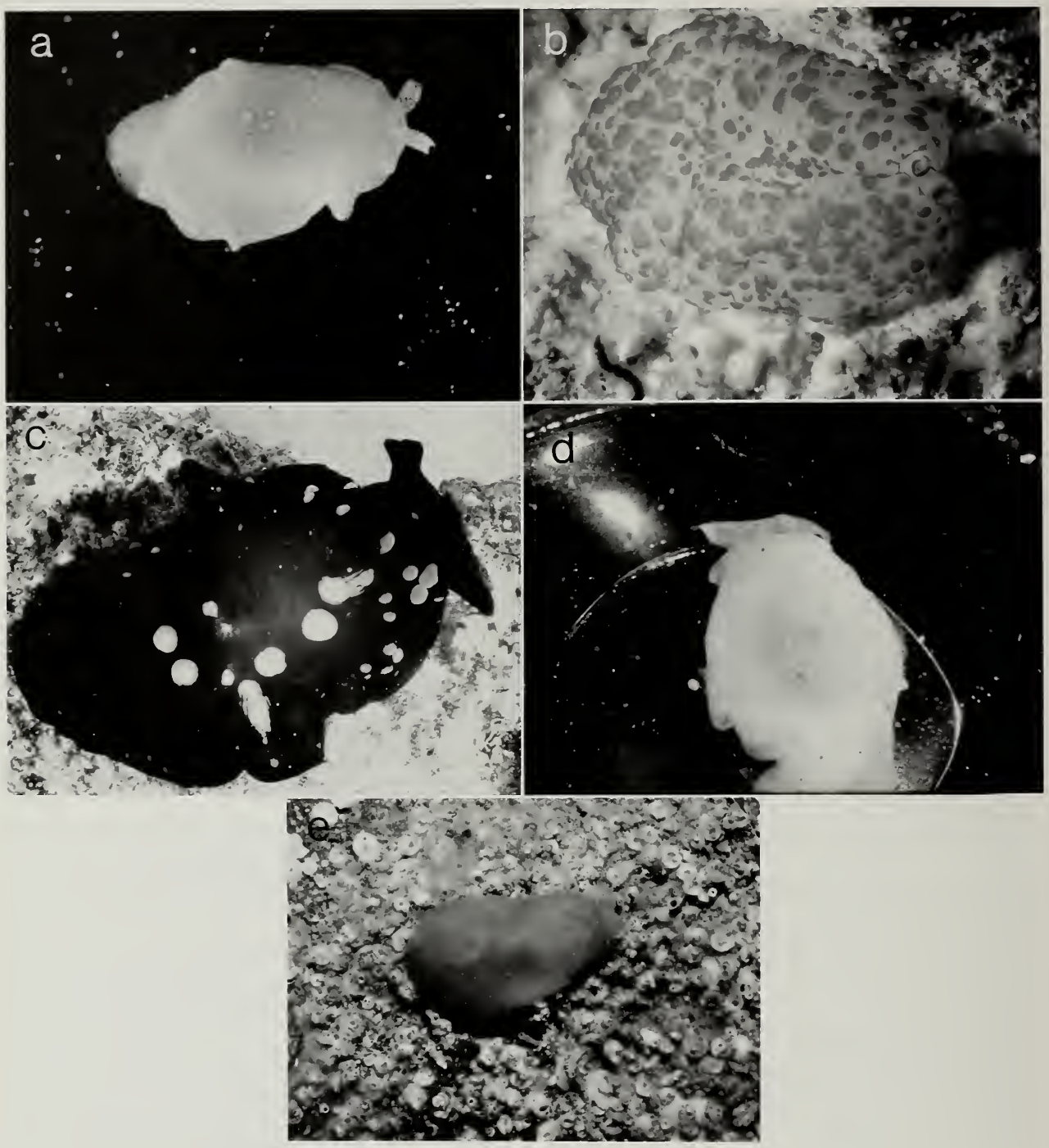

Figure 1

Living animals. A. *Berthella californica* (Dall, 1900), Duxbury Reef, Marin County, California, June 1968, photo by T.M.G. B. *Berthella martensi* (Pilsbry, 1896), Las Arenas, Baja California, 16 June 1985, photo by H.B. C. *Berthella martensi* (Pilsbry, 1896), Madang, Papua New Guinea, 2 October 1986, photo by T.M.G. D. *Berthella strongi* (MacFarland, 1966), Moss Beach, San Mateo County, California, 2 August 1966, photo by T.M.G. E. *Berthella agassizii* (MacFarland, 1909), Campitos, Punta Eugenia, Pacific coast of Baja California Sur, 30 June 1984, photo by T.M.G.

Figure 2

Berthella californica (Dall, 1900). Scanning electron micrographs. A. Jaw platelets, ×1100. B. Radular teeth from rachis, ×1500. C. Middle radular teeth, ×1500. D. Outer lateral teeth, ×1500.

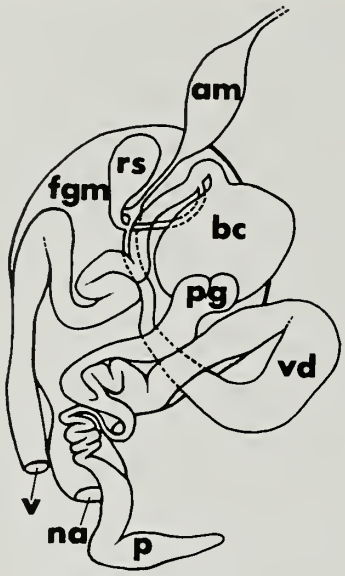

Figure 3

Berthella californica (Dall, 1900). Reproductive system: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; na, nidamental aperture; p, penis; pg, penial gland; rs, receptaculum seminis; v, vagina; vd, vas deferens.

are orange with dark brown lines and spots (Figure 1C), similar in pattern to that depicted by WILLAN (1984:fig. 25) from the Great Barrier Reef. The largest specimen examined in this study, collected in Papua New Guinea, was dark brown with lighter brown tubercles. The Panamanian specimens and the largest specimen from Papua New Guinea have autotomized portions of the mantle. The ctenidium is large, tripinnate, with 18–20 primary pinnae on either side of the rachis. The anus is located dorsal to the posterior limit of the attached portion of the ctenidium.

Internal morphology: The calcified portion of the shell was dissolved by fixative in all material we examined.

The jaws are well developed with numerous minute elements. The jaw elements (Figure 4) are most commonly unarmed, but in one of the Panamanian specimens a single denticle was present on some elements.

The radular formula was 58 × 62·0·62 in the animal from the Gulf of California and 83 × 95·0·95 in one of the Panamanian specimens. The inner teeth (Figure 5A) are simple and hook-shaped. A single basal denticle is present on some of the inner 10 teeth but is absent in others (Figure 5B). The central teeth are simple and elongate, becoming more hook-shaped towards the outer margin (Figures 5C, D).

The reproductive system (Figure 6) is androdiaulic. Its morphology was identical in one specimen from Panama and one from Papua New Guinea. The ampulla is elongate, curved, and muscular. It divides distally into the short oviduct and the vas deferens. The oviduct enters the female gland mass near the albumen gland. The vas deferens is glandular for most of its length, but does not expand into a thickened prostatic gland. Near its distal end it joins with the elongate, curved penial gland and narrows into a short ejaculatory segment prior to entering the penial sac. The pyriform receptaculum seminis and the spherical bursa copulatrix join the vaginal duct near the middle of its length. The vaginal opening is immediately ventral to the penis.

Discussion: The variability of the living animal and the anatomy of *Berthella martensi* were recently reviewed (WILLAN, 1984). One of the chief distinguishing features of this species is the presence of "preformed shear zones" where portions of the mantle may be autotomized. In his discussion of this species, Willan noted that *B. kaniae* Sphon, 1972, also autotomizes portions of its mantle. Willan suggested that it differs from *B. martensi* in not having distinct shear zones and in having a more shallowly cleft anterior margin of the mantle. However, specimens examined in this study indicate that Panamic specimens also have preformed areas where autotomy occurs. Similarly, the mantle is as deeply cleft in these specimens as in Willan's figures (1984:figs. 21–25) of *B. martensi*. The jaws and radula of the present material agree well with those described for *B. martensi*. Willan noted that *B. martensi* lacks a vas deferens expanded into a distinct prostate gland. The present material also lacks a distinct prostate. There is no basis for maintaining the separation of *B. kaniae* Sphon, 1972, and it is here regarded as a junior synonym of *B. martensi* (Pilsbry, 1896).

Berthella stellata (Risso, 1826)

(Figures 7–12)

Pleurobranchus stellatus RISSO, 1826:41.
Berthella stellata (Risso, 1826): PRUVOT-FOL, 1954:223.
Pleurobranchus pellucidus PEASE, 1860:24; syn. nov.
Berthella pellucida (Pease, 1860): THOMPSON, 1970:188; syn. nov.
Berthella tupala ER. MARCUS, 1957:416, figs. 58–69; syn. nov.
Berthella postrema Burn, 1962: WILLAN, 1984:42.
Berthella stellata albocrossata HELLER & THOMPSON, 1983: 328, figs. 5A–C; syn. nov.

Distribution: *Berthella stellata* was originally described from the Mediterranean (RISSO, 1826; THOMPSON, 1981). It has also been recorded from the Indo-Pacific tropics from South Africa (GOSLINER, 1987, as *B. tupala*), the Sudanese Red Sea (HELLER & THOMPSON, 1983, as *B. stellata albocrossata*), Australia (BURN, 1962, as *B. postrema*; THOMPSON, 1970, and WILLAN, 1984, as *B. pellucida*), New Caledonia (RISBEC, 1928, as *B. pellucida*) and Hawaii (PEASE, 1860, and KAY, 1979, as *B. pellucida*). In the eastern Pacific this species occurs from the Pacific coast of Baja California and from several localities within the Gulf of California (present study). The species has been recorded from several localities within the Caribbean (as *B. tupala*): Brazil (ER. MARCUS, 1957); Florida (EV. MARCUS

Figure 4

Berthella martensi (Pilsbry, 1896). Scanning electron micrographs of jaw platelets from different portions of the same jaw of the specimen from Las Arenas. A. ×1300. B. ×1500.

Figure 5

Berthella martensi (Pilsbry, 1896). Scanning electron micrographs of radula. A. Dorsal view of rachis of Las Arenas specimen, ×1700. B. Lateral view of rachis of Panamanian specimen, ×1300. C. Middle lateral teeth of Panamanian specimen, ×1000. D. Outer lateral teeth of Las Arenas specimen, ×1700.

& Er. Marcus, 1967); Puerto Rico (Er. Marcus & Ev. Marcus, 1970a); Panama (Bertsch, 1975); Colombia (Ev. Marcus, 1984). We report its occurrence from the Caribbean, Gulf of California, and Pacific coasts of Mexico. Thus, *B. stellata* has a circumtropical distribution.

Material: Two specimens, California Academy of Sciences, San Francisco, CASIZ 064827, intertidal zone, Fokea, Greece, 13 June 1986, T. E. Thompson. One specimen, CASIZ 063274, 1 m depth, eastern shore of Laguna de Nichupte, Cancun, Quintana Roo, Mexico (21°25′N, 86°50′W), 2 January 1978, T. M. Gosliner. One specimen, CASIZ 064832, 7 m depth, W side of point of Fort Jeudy, Grenada (11°59′N, 61°42′W), 24 August 1986, H. Bertsch. One specimen, CASIZ 063277, intertidal zone, Centro de Acuacultura, Bahía Tortugas, Baja California Sur, Mexico (27°42′N, 114°53′W), 2 July 1984, H. Bertsch. One specimen, CASIZ 064834, Isla Coronado, Bahía de los Angeles, Baja California, Mexico (29°03′N, 113°31′W), 27 April 1986, H. Bertsch. One specimen, CASIZ 064830, 10 m depth, Punta Gringa, Bahía de los Angeles, Baja California, Mexico, 29 June 1987, S. Millen. One specimen, CASIZ 064825, 3 m depth, El Embudo, Isla Partida, Baja California Sur, Mexico (24°32′N, 110°23′W), 23 July 1985, T. M. Gosliner. One specimen, CASIZ 063275, under rock in seawater tables, Hawaii Institute of Marine Biology, Coconut Island, Oahu, Hawaiian Islands (21°32′N, 157°40′W), 26 October 1986, T. M. Gosliner. One specimen, CASIZ 064833, intertidal zone, under rocks, Hastings Point, New South Wales, Australia, October 1986, R. C. Willan and T. M. Gosliner. One specimen, South African Museum, Cape Town, SAM A35259, intertidal zone, under large rock, Umgazana, Transkei, South Africa (31°37′S, 29°32′E), 28 October 1981, T. M. Gosliner.

External morphology: The living animals examined in this study (Figure 7) reached a maximum length of 20 mm. The body is generally translucent white to honey brown. Scattered, small opaque white markings are present on the notum. An opaque white transverse bar or cross is generally situated near the middle of the notum, but may be entirely absent in specimens from several localities. In one specimen collected by one of us (H.B.) from Puerto Peñasco, Mexico, a yellow tubercle was present on either limit of the opaque white transverse bar. The ctenidium is bipinnate with up to 17 primary pinnae on either side of the rachis. The anus is situated dorsal to the posterior limit of the gill membrane.

Internal morphology: The shell (Figure 8) is elongate with faint to well developed longitudinal and axial sculpture.

The jaws are strongly developed with numerous chitinous elements (Figure 9). The shape and dentition of these elements vary considerably, even within a single jaw (Figures 9E, F, Table 1). There are 1–6 denticles on either side of the jaw elements in the present material.

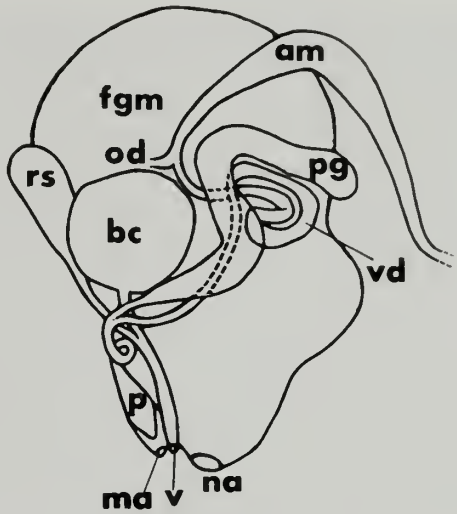

Figure 6

Berthella martensi (Pilsbry, 1896). Reproductive system: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; ma, male aperture; na, nidamental aperture; od, oviduct; p, penis; pg, penial gland; rs, receptaculum seminis; v, vagina; vd, vas deferens.

The radular formula exhibited considerable variation in the individual specimens examined in this study (Table 1). The combined formula is 50–80 × 45–72·0·45–72. The inner lateral teeth are simple and hook-shaped (Figure 10). A basal denticle is present on some of the inner teeth in specimens from Cancun (Mexico) and Umgazana (South Africa) (Figure 10C). The length of the cusp of the radular teeth increases towards the margin. In all specimens the outer 4–10 lateral teeth are elongate and possess a secondary denticle, in addition to the main cusp (Figure 11). In the specimen from Bahía de los Angeles and the animals from Greece, the outermost teeth are not elongate, but still have a secondary denticle.

The reproductive system (Figure 12) is androdiaulic. The ampulla is elongate and curved, but not convoluted. It bifurcates distally into a short oviduct and the vas deferens. The oviduct enters the female gland mass near the albumen gland. The vas deferens expands into a thickened prostate and narrows again distally, just prior to its juncture with the penial gland. The penial gland is shortest in the specimen from Cancun and most elongate and convoluted in the Hawaiian specimen. The penis is short and muscular. The receptaculum seminis is pyriform and lightly pigmented in all specimens examined. The duct of the receptaculum seminis may be short or elongate, and may enter the vaginal duct at the base of the spherical bursa copulatrix or near the middle of the vagina. The vaginal duct exits immediately ventral to the penis.

Discussion: Several species of *Berthella* with scattered or medially situated opaque white markings have been considered as distinct for many years (Risso, 1826; Pease, 1860; MacFarland, 1909; Er. Marcus, 1955, 1957;

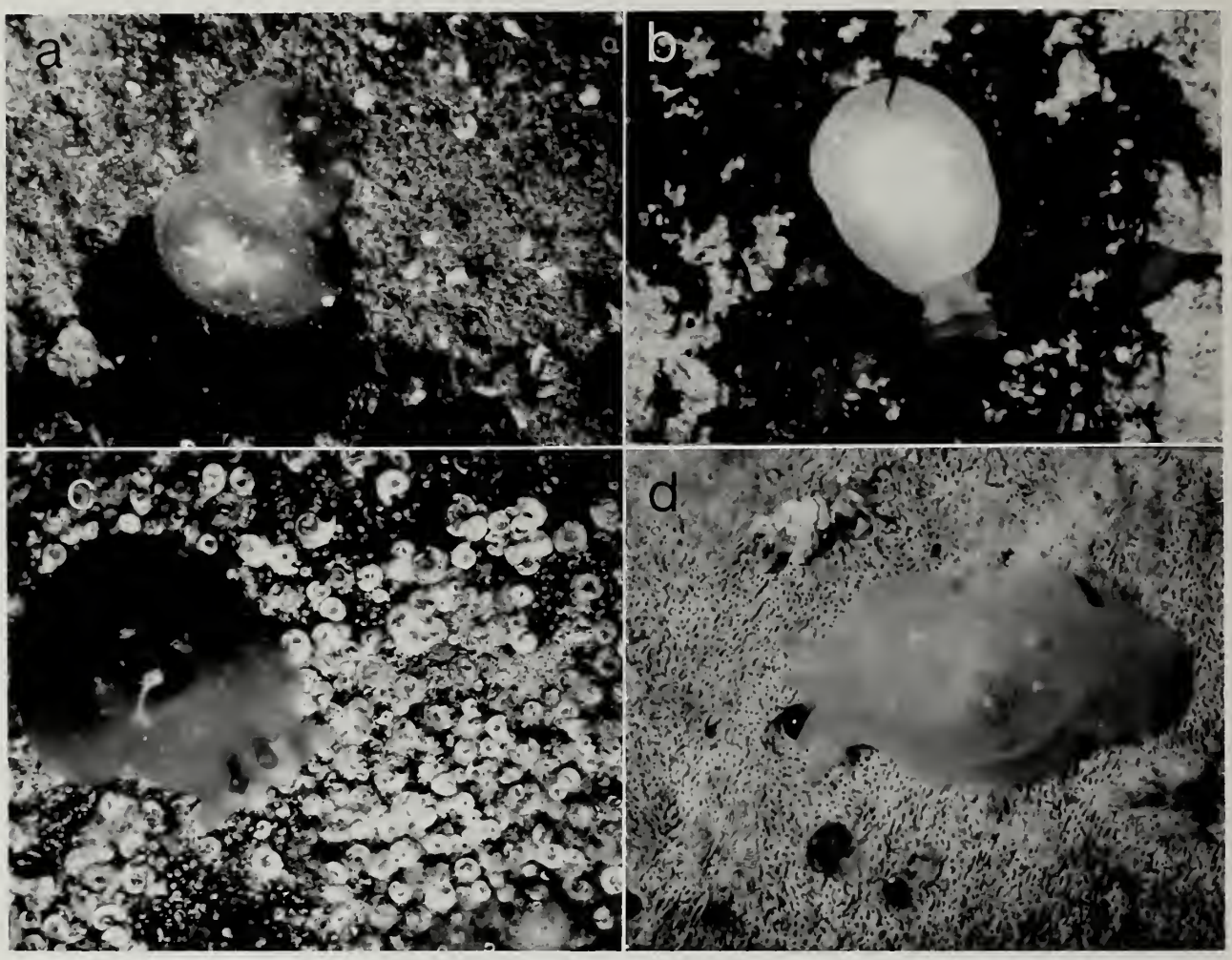

Figure 7

Berthella stellata (Risso, 1826). Living animals. A. Specimens from Puerto Peñasco, Sonora, Gulf of California coast of Mexico. B. Specimen from Umgazana, Transkei, South Africa. C. Specimen from Bahía Tortugas, Baja California Sur, Pacific coast of Mexico. D. Specimen from Hastings Point, New South Wales, Australia.

Thompson, 1981; Heller & Thompson, 1983; Ev. Marcus, 1984). Bertsch (1975) and Willan (1984) have shown that certain characters, particularly the elaboration of jaw elements, may vary considerably within single populations or individuals of *Berthella* species.

In attempting to identify specimens of *Berthella* from various localities on both coasts of Baja California, it became apparent that a critical review of species with similar markings was necessary to establish the identity of this material. Material from the Aegean Sea of Greece, the western Atlantic of Mexico, Grenada and Brazil, the Hawaiian Islands, Australia, and South Africa was examined in addition to the Baja Californian material. Table 1 indicates the range of morphological variability present in material examined in this study and known from the literature.

The color of specimens varies greatly. In almost all cases the body is translucent whitish to yellowish brown. The presence or absence of opaque white pigment and its variable arrangement has been noted by numerous authors. Thompson (1985; personal communication) has documented considerable variability in the arrangement of opaque white pigment of Aegean specimens. He also noted that occasional yellow tubercles may be present, as in the specimen from Puerto Peñasco described above.

The anus is always situated at the posterior end of the gill membrane.

The shell of *Berthella stellata* in all material, when preserved, is well developed with faint to well developed sculpture. The length relative to the width, though not quantified, varies considerably.

The shape and denticulation of the jaw elements varies markedly. There is significant variation even between different portions of a single jaw (Figures 9E, F). Willan

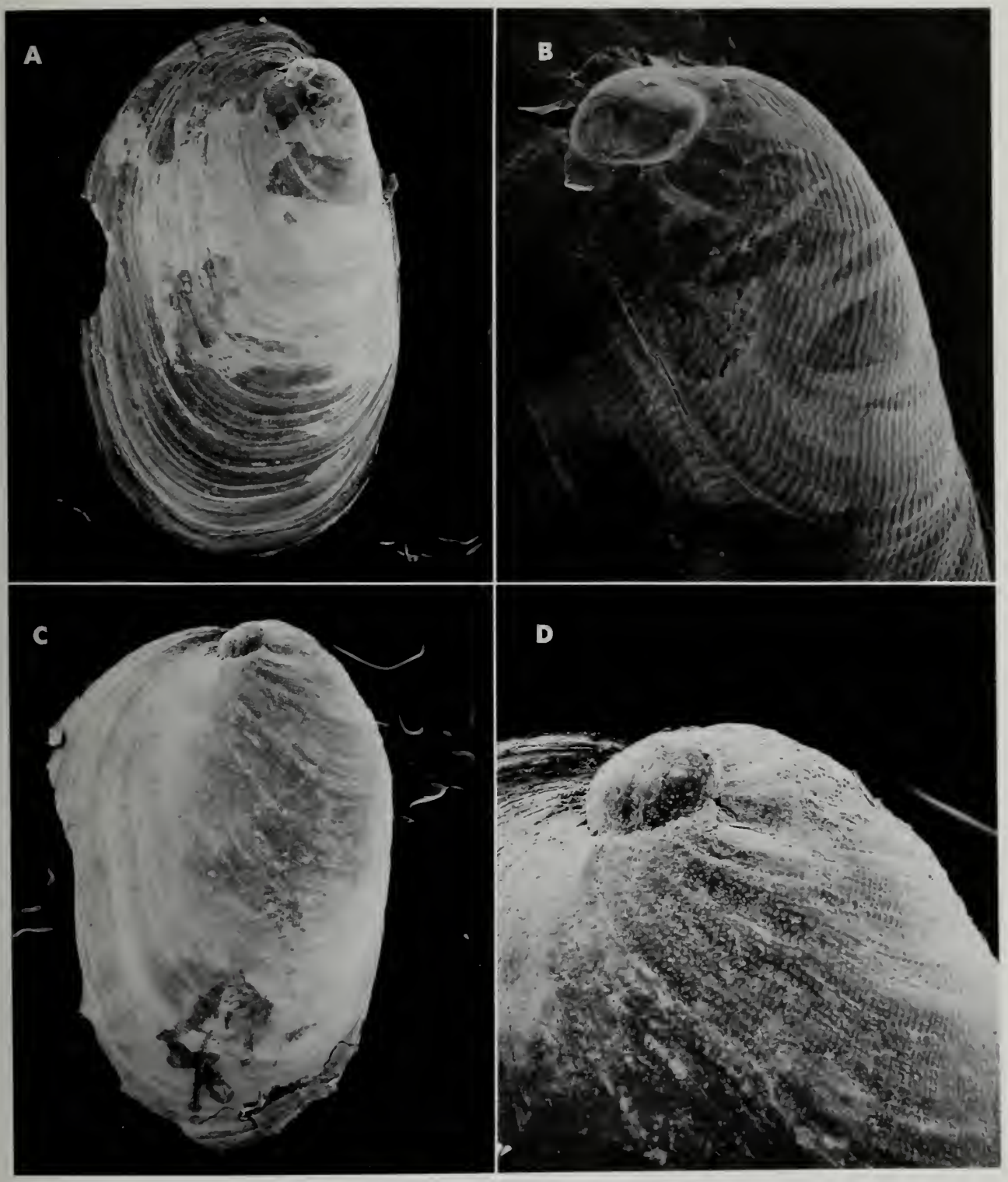

Figure 8

Berthella stellata (Risso, 1826). Scanning electron micrographs of shells with detail of sculpture and protoconch. A. ×22. B. ×100, specimen from Bahía Tortugas, Baja California Sur, Pacific coast of Mexico. C. ×25. D. ×70, specimen from Coconut Island, Oahu, Hawaiian Islands.

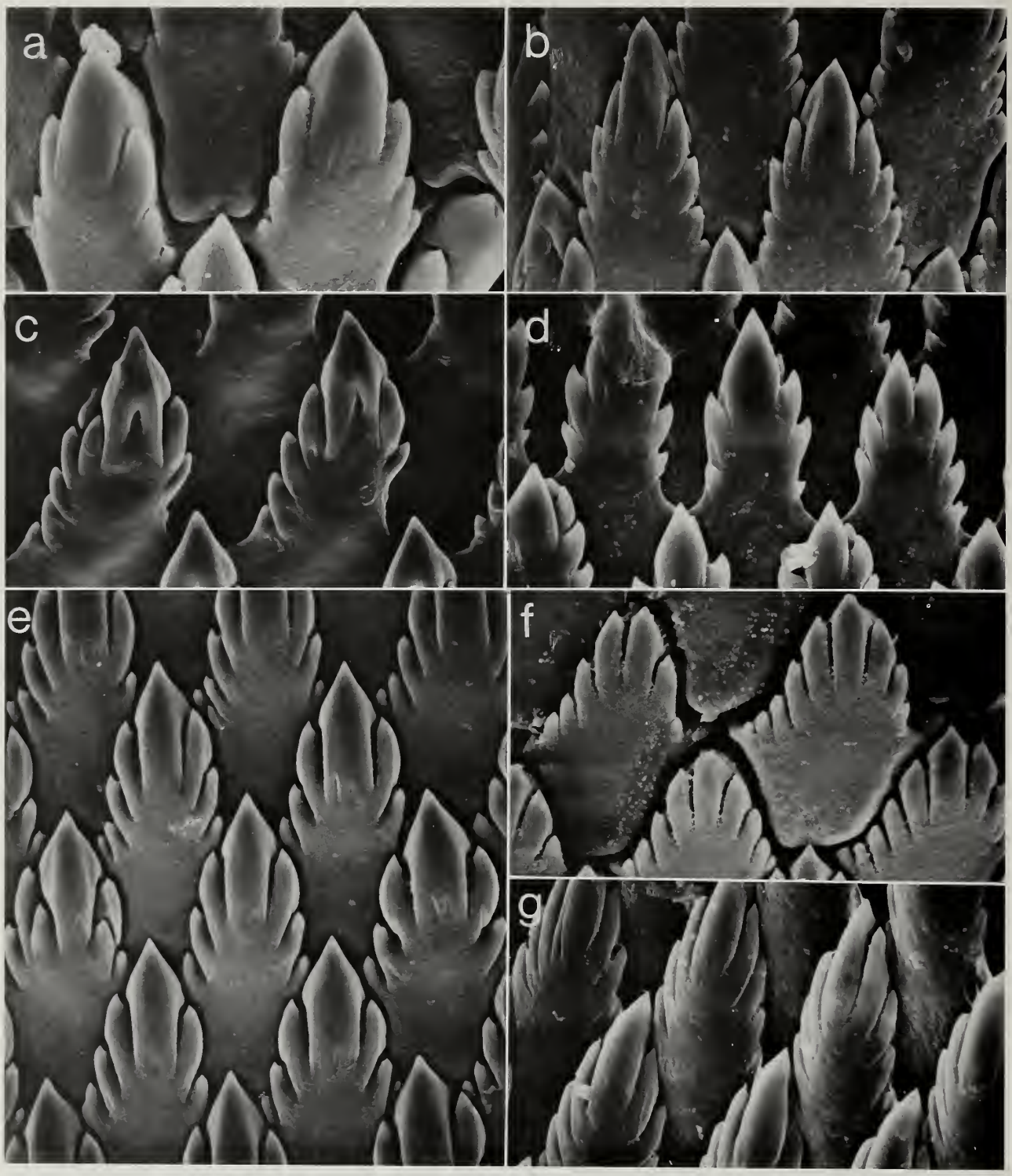

Figure 9

Berthella stellata (Risso, 1826). Scanning electron micrographs of jaw platelets. A. Small specimen from Fokea, Greece, ×1700. B. Large specimen from Fokea, Greece, ×1000. C. Specimen from Cancun, Quintana Roo, Caribbean coast of Mexico, ×1700. D. Specimen from Bahía de los Angeles, Baja California, Gulf of California coast of Mexico, ×1500. E and F. Different portions of same jaw of specimen from Coconut Island, Oahu, Hawaiian Islands, both ×2000. G. Specimen from Hastings Point, New South Wales, Australia, ×1480.

Table 1

Morphological variability in *Berthella stellata*.

Specimen	Color	Shell	Radular formula	Inner laterals	Outer laterals	Receptaculum seminis	Jaw denticle	Entrance of rs duct into vagina	Locality	Reference
Berthella tupala	ochre with opaque white trapezoid and spots	broad, with moderate sculpture	55 × 50·0·50	denticle on inner tooth	6–8 outer teeth bifid	absent	0–5	—	Brazil	MARCUS, 1957, 1967; MARCUS & MARCUS, 1970a
B. tupala	yellowish with opaque white "T"	broad, with distinct sculpture	—	1st three laterals with basal denticle	—	—	0	—	Panama	BERTSCH, 1975
B. pellucida	pale honey brown with opaque white cross and/or spots	broad, without marked sculpture	57 × 55·0·55 61 × 58·0·58 60 × 45·0·45	simple hooks, no dentricles	some bifid	no pigment noted	—	base of bursa	Enewetak, Marshall Is.	WILLAN, 1984
B. stellata	translucent white with scattered opaque white spots	broad, with moderate sculpture	56 × 49·0·49	no denticles	outer 9–10 teeth bifid	light	1–5	base of bursa	Hawaii	present study
B. stellata	translucent white with opaque white bar	dissolved	50 × 55·0·55	some denticles	bifid	light	1–5	middle of vagina	Cancun	present study
B. stellata	translucent white with scattered opaque white spots	narrow, with sculpture	57 × 59·0·59	no denticles	bifid	light	2–5	middle of vagina	Bahía Tortugas, Pacific coast Baja Calif.	present study
B. stellata	—	dissolved	61 × 61·0·61	no denticles	some bifid	light	2–5	into middle of vagina	Bahía de Los Angeles, Gulf coast of Baja Calif.	present study
B. tupala	translucent white with opaque white bar and scattered spots	broad, with moderate sculpture	54 × 61·0·61	some denticles	bifid	light	0–5	—	South Africa	GOSLINER, 1987
B. stellata	white ? honey with opaque white spots	faint sculpture	65 × 54·0·54 72 × 63·0·63	no denticles	some bifid	light	2–5	base of bursa	N.S.W., Australia	present study
B. stellata	whitish with opaque white	faint sculpture	58 × 62·0·62 72 × 62·0·62	—	—	—	—	—	Yugoslavia	THOMPSON, 1985
B. stellata albocrossata	off-white with opaque white cross	absent	51 × 51·0·51	—	—	—	4	—	Sudanese Red Sea	HELLER & THOMPSON, 1983
B. stellata	—	faint sculpture	52 × 57·0·57 80 × 72·0·72	no denticles	some bifid	light	2–6	middle of vagina	Greece	present study

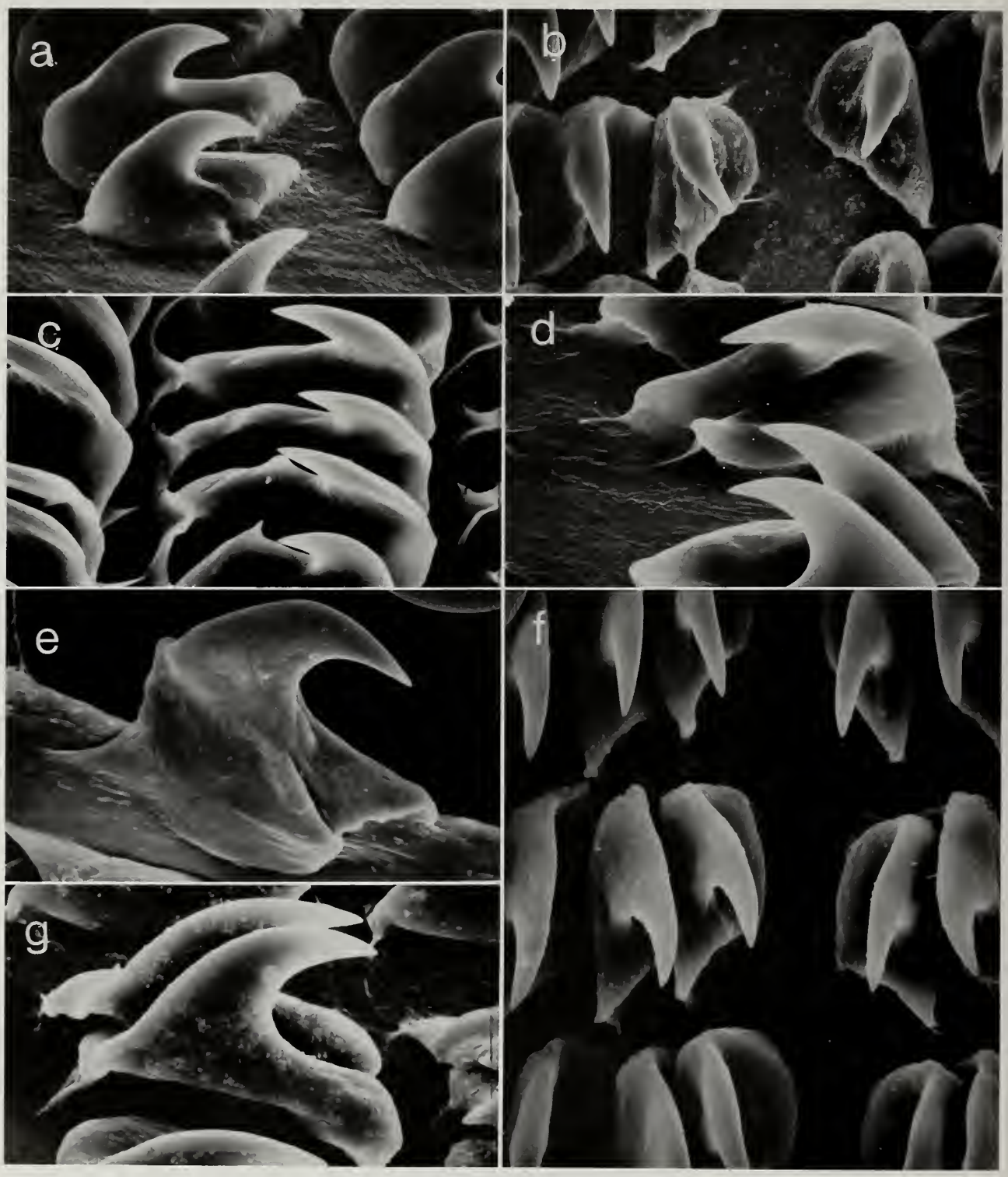

Figure 10

Berthella stellata (Risso, 1826). Scanning electron micrographs of rachis and innermost teeth. A. Small specimen from Fokea, Greece, ×2500. B. Large specimen from Fokea, Greece, ×1700. C. Specimen from Cancun, Quintana Roo, Caribbean coast of Mexico, ×3500. D. ×3000. E. Specimens from Bahía de los Angeles, Baja California, Gulf of California coast of Mexico, ×2000. F. Specimen from Hastings Point, New South Wales, Australia, ×2000. G. Specimen from Coconut Island, Oahu, Hawaiian Islands, ×5000.

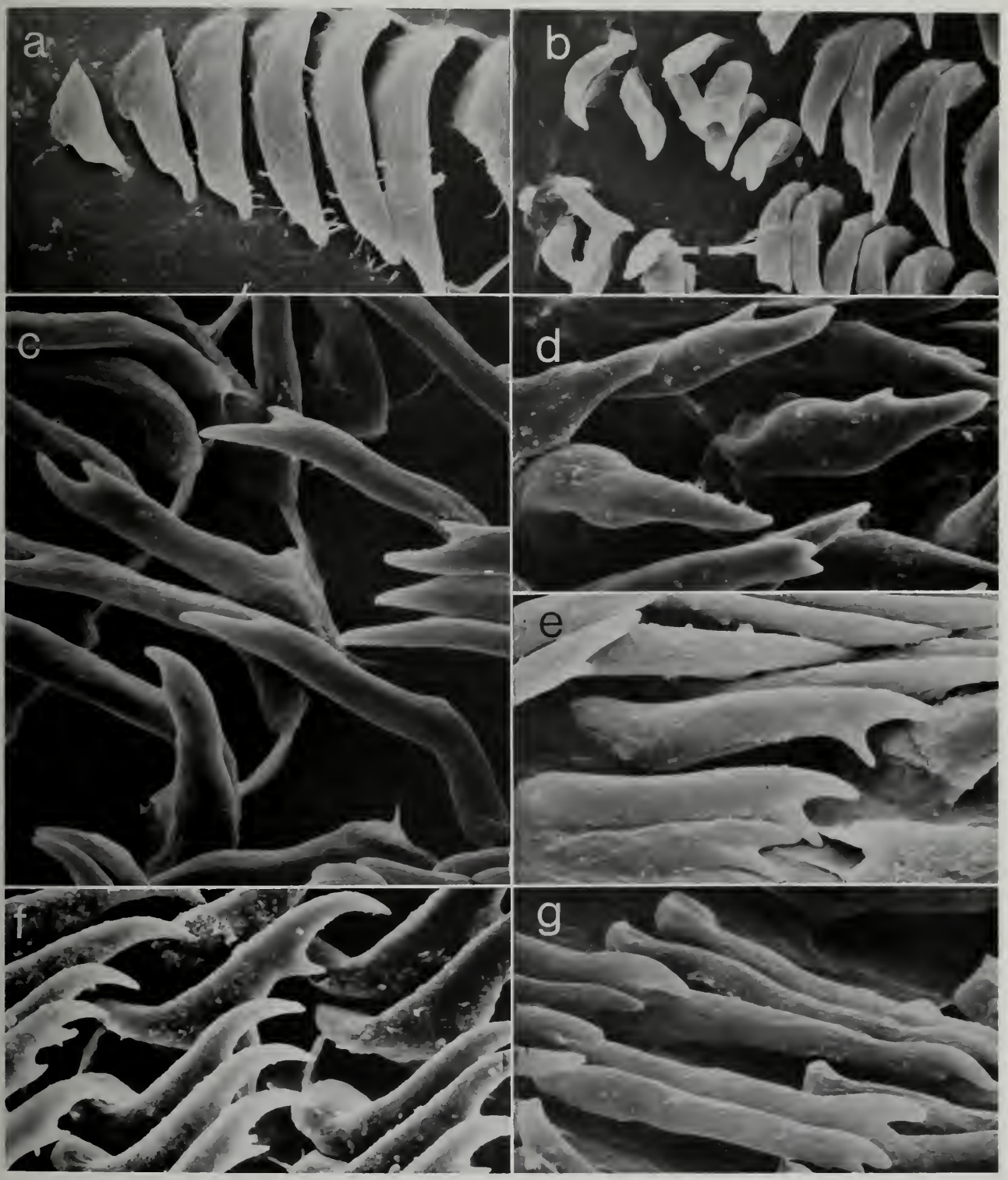

Figure 11

Berthella stellata (Risso, 1826). Scanning electron micrographs of outermost radular teeth. A. Small specimen from Fokea, Greece, ×2200. B. Large specimen from Fokea, Greece, ×1500. C. Specimen from Cancun, Quintana Roo, Caribbean coast of Mexico, ×3000. D. Specimen from Bahía de los Angeles, Baja California, Gulf of California coast of Mexico, ×2000. E. Specimen from Bahía Tortugas, Baja California Sur, Pacific coast of Mexico, ×4000. F. Specimen from Coconut Island, Oahu, Hawaiian Islands, ×2500. G. Specimen from Hastings Point, New South Wales, Australia, ×2500.

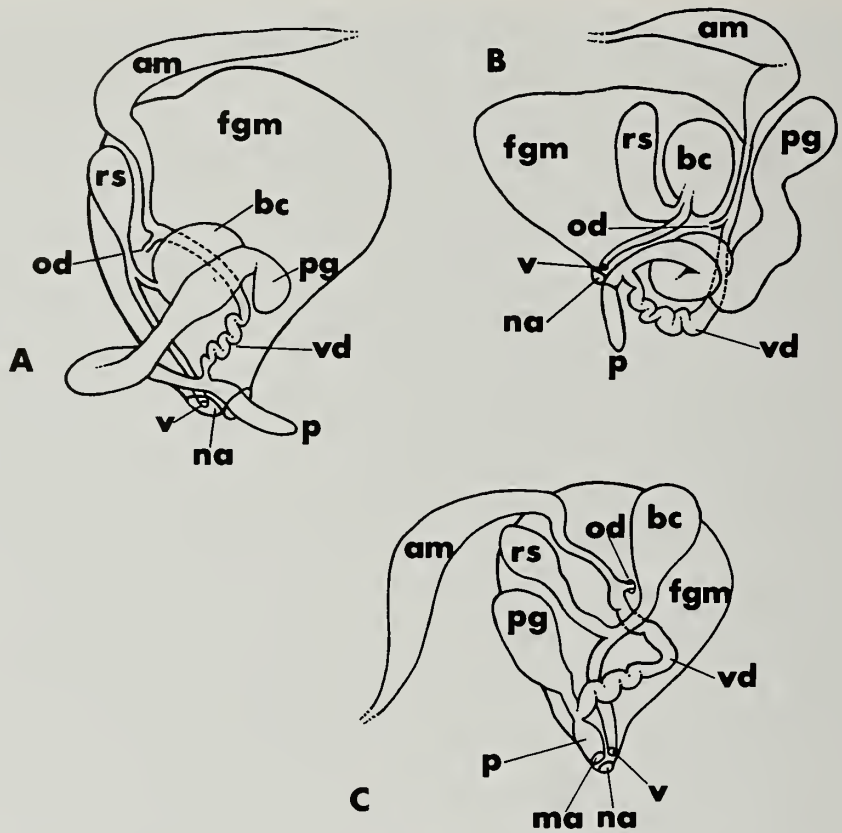

Figure 12

Berthella stellata (Risso, 1826). Reproductive systems. A. Specimen from Fokea, Greece. B. Specimen from Coconut Island, Oahu, Hawaiian Islands. C. Specimen from Cancun, Quintana Roo, Caribbean coast of Mexico. Key: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; ma, male aperture; na, nidamental aperture; od, oviduct; p, penis; pg, penial gland; rs, receptaculum seminis; v, vagina; vd, vas deferens.

(1984) noted the variability in the number of denticles of jaw elements of various species of *Berthella,* including *B. pellucida* and *B. tupala.* None of the material examined in the present study entirely lacked denticles.

The radular formula varied slightly in all accounts. Considerable variation was present, however, in the shape and secondary denticulation of the inner and outer radular teeth. In all specimens, the inner teeth are short and hook-shaped. On some teeth there is a secondary denticle, but this is inconsistent even within a single individual. The teeth are more elongate towards the outer margin, and a secondary denticle is present on the cusp of the outer teeth, in all material examined.

The reproductive morphology is uniform throughout the material studied, with a few minor exceptions. The duct of the receptaculum seminis may join the vagina at the base of the bursa copulatrix, or near the middle of the vaginal duct (Table 1). The length of the penial gland also varies slightly.

Studies on the systematics of *Berthella* have focused on minute differences between species. This is particularly true of material described from the Caribbean (Ev. Marcus, 1984). Part of the confusion stems from the fact that several species have been incompletely or incorrectly described. The reproductive anatomy of *B. stellata* has never been described. The description of *B. tupala* (Er. Marcus, 1957) indicates that a receptaculum seminis is absent and that the uterine duct enters the female gland mass. No other known species lacks a receptaculum seminis or has any connection of either the receptaculum or bursa copulatrix directly with the female gland mass. The fact that the specimen from Cancun examined in this study agreed with Marcus' description of *B. tupala,* but had a more typical arrangement of reproductive organs, with a receptaculum seminis, suggests that the original description of the arrangement of reproductive organs was in error.

When one examines the morphological variability of these species of *Berthella* (Table 1) several facts become apparent. (1) Much of the variation exhibited throughout the world is expressed in individuals within a single limited geographical area, such as Baja California. (2) There is

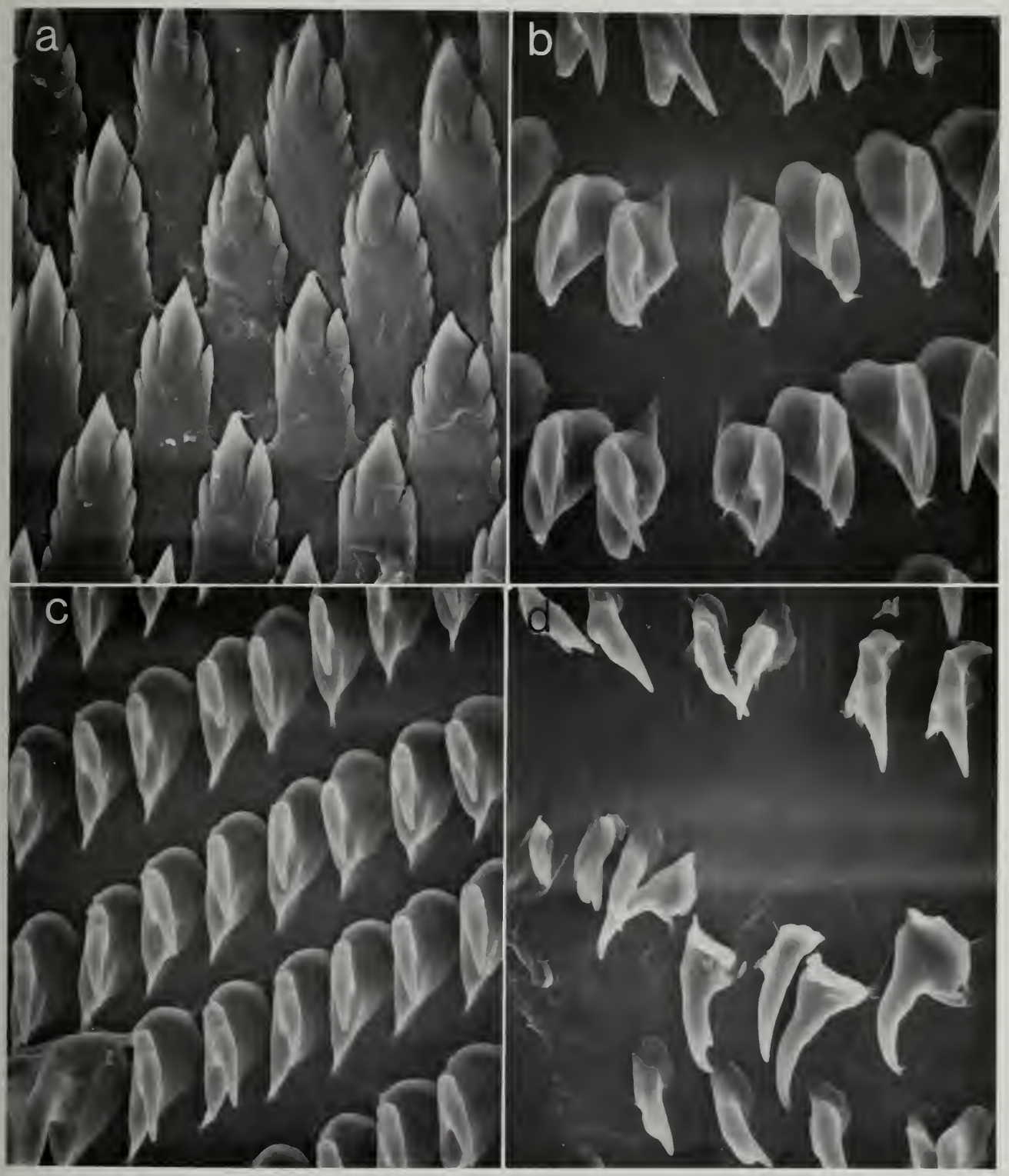

Figure 13

Berthella strongi (MacFarland, 1966). Scanning electron micrographs. A. Jaw platelets, ×1190. B. Rachis of radula, ×1700. C. Middle of radula, ×1300. D. Outer radular teeth, ×3000.

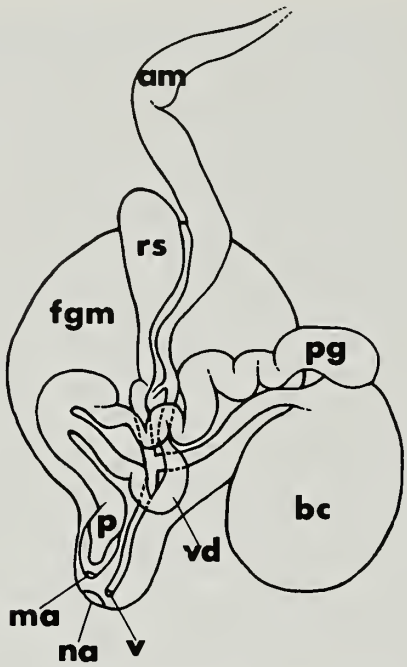

Figure 14

Berthella strongi (MacFarland, 1966). Reproductive system: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; ma, male aperture; na, nidamental aperture; p, penis; pg, penial gland; rs, receptaculum seminis; v, vagina; vd, vas deferens.

little consistency in the correlation of variable characters. (3) There is little correlation between morphological variability and specific geographical regions.

Based on these facts one can arrive at several conclusions. (1) Each variant with a different set of characters must be considered as a distinct species. (2) Several species are widespread and are often sympatric. (3) Only one variable, circumtropical species exists. It is far more parsimonious and biologically realistic to consider *Berthella pellucida* (and its synonyms listed by WILLAN, 1984), *B. tupala,* and *B. stellata albocrossata* all as junior synonyms of *B. stellata.*

Berthella tamiu Ev. Marcus, 1984, is also found from the Caribbean, though from deeper water than *B. stellata.* It differs from *B. stellata* in several important regards. All of the jaw elements are edenticulate. The radula contains all hook-shaped teeth, as opposed to elongate and, often, bifid outer lateral teeth of *B. stellata.* The penial papilla of *B. tamiu* is far more elongate than that of *B. stellata.*

Berthella strongi (MacFarland, 1966), comb. nov.

(Figures 1D, 13, 14)

Pleurobranchus strongi MACFARLAND, 1966:89, pl. 6, figs. 3–7, pl. 15, figs. 1–15, pl. 16, figs. 13, 14.

Distribution: Moss Beach (San Mateo County) to Santa Cruz Island (Santa Barbara County), California (BEHRENS, 1980).

Material: One specimen, CASIZ 064826, intertidal zone, Moss Beach, San Mateo County, California (37°32′N, 122°31′W), 2 August 1966, G. C. Williams and T. M. Gosliner. One specimen, CASIZ 064822, intertidal zone, Great Tide Pool, Pacific Grove, Monterey County, California (36°37′N, 121°54′W), July 1921, F. M. MacFarland.

External morphology: The living animal from Moss Beach (Figure 1D) was approximately 25 mm in length. It was beige with a few scattered opaque white spots. The ctenidium, while simply plicate, has 16 primary pinnae. No obvious tubercles are present along the gill rachis.

Internal morphology: The shell of the specimen from Moss Beach was entirely decalcified and the shell of the specimen from Pacific Grove had been removed by dissection (from MacFarland's notes), but was not with the specimen.

The jaws are ornamented with numerous elements (Figure 13A) bearing 1–5 denticles on either side of the central cusp. The radula has a formula of 62 × 69·0·69 and 61 × 64·0·64 in the two specimens examined. In both cases the innermost teeth (Figure 13B) have a short cusp and are steeply arched. The teeth become more elongate towards the outer margin of the radula, but diminish again in length in the outer 5–7 teeth (Figure 13C). Some secondary denticles were observed in a specimen from Diablo Cove (Figure 13D).

The reproductive system (Figure 14) is androdiaulic and was identical in its configuration in the two specimens examined. The ampulla is straplike and thick. It narrows proximally and divides into the short oviduct and the vas deferens. The female gland mass is well developed, with the mucous gland forming the largest portion of the nidamental glands. The muscular receptaculum seminis is pyriform and possesses an elongate duct. The receptaculum duct joins the vagina near the middle of its length between the large, spherical bursa copulatrix and the gonopore. The vas deferens is prostatic throughout most of its length. The prostate joins with the elongate convoluted penial gland and together they enter the muscular, conical penial papilla.

Discussion: The present material agrees in all respects with MACFARLAND's (1966) and BEHRENS' (1980) descriptions of this species. By virtue of the facts that the gill rachis lacks distinct tubercles and an elongate penial gland is present, this species is transferred from *Pleurobranchus* to *Berthella.*

Berthella strongi is similar to *B. stellata* in several aspects of its morphology. However, there are consistent differences, which clearly differentiate the species. The radular teeth of *B. strongi* (Figure 13) have a narrower, more elongate cusp than any of those found in *B. stellata* (Figures 10, 11). The outer teeth of *B. strongi* are never elongate or bifid. Most significantly, the penial gland of *B. strongi* (Figure 14) is always highly convoluted, while that of *B.*

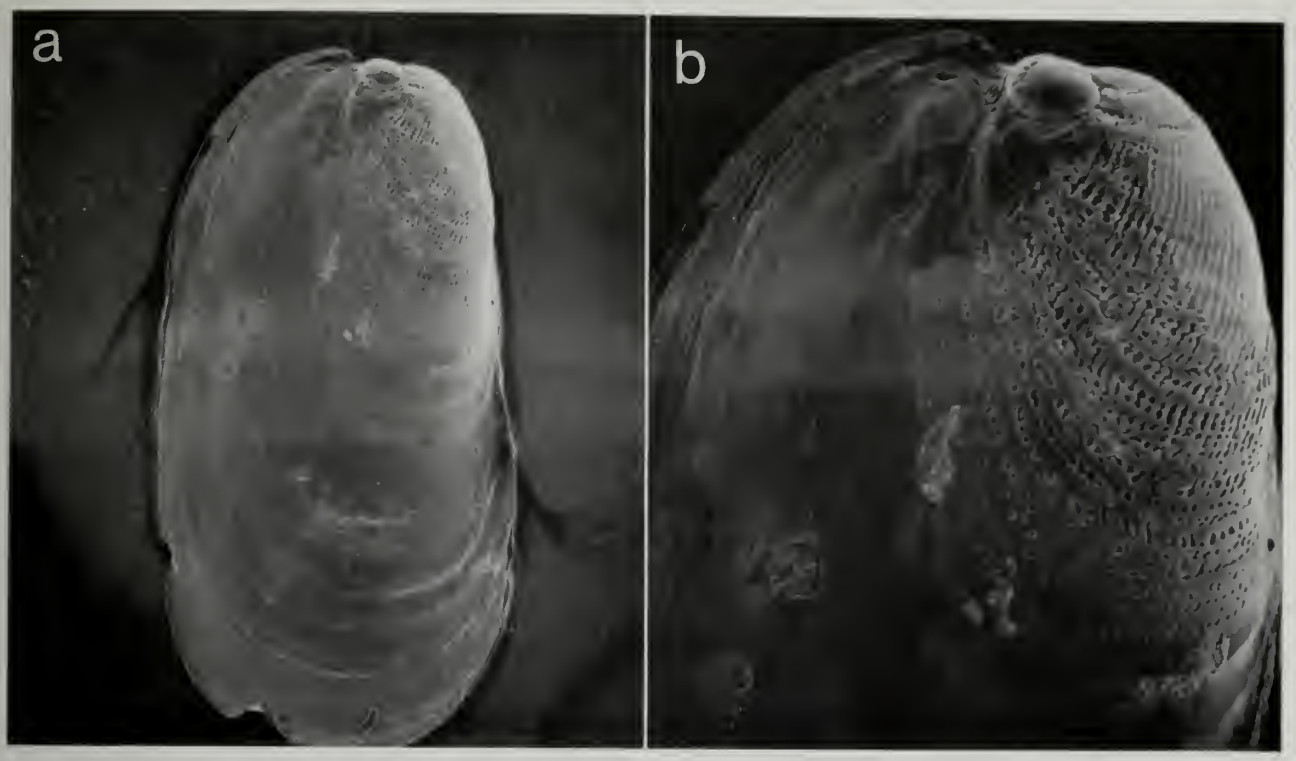

Figure 15

Berthella agassizii (MacFarland, 1909). Scanning electron micrographs of shell of specimen from Campitos, Punta Eugenia, Pacific coast of Baja California Sur. A. Entire shell, ×30. B. Close up of shell showing protoconch and sculpture, ×60.

stellata (Figure 12) has a maximum of one or two convolutions.

Berthella agassizii (MacFarland, 1909)

(Figures 1E, 15–18)

Pleurobranchus agassizii MacFarland, 1909:59, pl. 11, figs. 43–54, pl. 12, figs. 55–57.
Bouvieria agassizii (MacFarland, 1909): Engel, 1927:110, figs. 26a–c.
Berthella agassizii (MacFarland, 1909): Er. Marcus, 1955: 117, figs. 66–77; Ev. Marcus, 1984:51, figs. 6–16.

Distribution: This species has been recorded from several localities within the Caribbean, southwards to Brazil (Ev. Marcus, 1984) and is here recorded from both coasts of Baja California.

Material: Holotype (CASIZ 021162) and paratype (CASIZ 021163) of *Pleurobranchus agassizii,* both collected from Riacho Doce, Alagoas, Brazil, 1899?, A. W. Greely. One specimen, CASIZ 063276, 3 m depth, Campitos, 20 km east of Punta Falsa, Baja California, Mexico (27°50′N, 114°50′W), 30 June 1984, T. M. Gosliner. One specimen, CASIZ 063278, 6 m depth, southern end of Bahía Pulmo, Baja California Sur, Mexico (23°24′N, 109°24′W), 22 January 1984, T. M. Gosliner.

External morphology: The living animals (Figure 1E) reached a maximum of 12 mm in length. The specimen from Campitos was reddish brown with scattered opaque white spots. The individual collected from Cabo Pulmo was translucent pink with scattered opaque white spots. The gill is bipinnate with up to 15 primary pinnae on either side of the central rachis. The anus, in the three specimens examined, is situated on an elevated papilla dorsal to the middle of the gill membrane.

Internal morphology: The shell (Figure 15) is narrow. Only the older portions bear sculpture.

The jaws are well developed with numerous minute elements. The elements (Figures 16A, 17A) bear 1–6 denticles on either side of the central cusp.

The radular formula is 45–52 × 42–53·0·42–53 in three specimens examined. The inner lateral teeth (Figures 16B, 17B, C) are simply hook-shaped, without auxiliary denticles. The middle teeth of each half row (Figure 16C) are larger, but essentially the same shape as the inner teeth. The outermost teeth (Figures 16D, 17D) are simple, small hooks, without a secondary denticle.

The reproductive system (Figure 18) is androdiaulic. The thick, slightly convoluted ampulla narrows distally and divides into the short oviduct and an elongate, prostatic vas deferens. The vas deferens narrows prior its junction

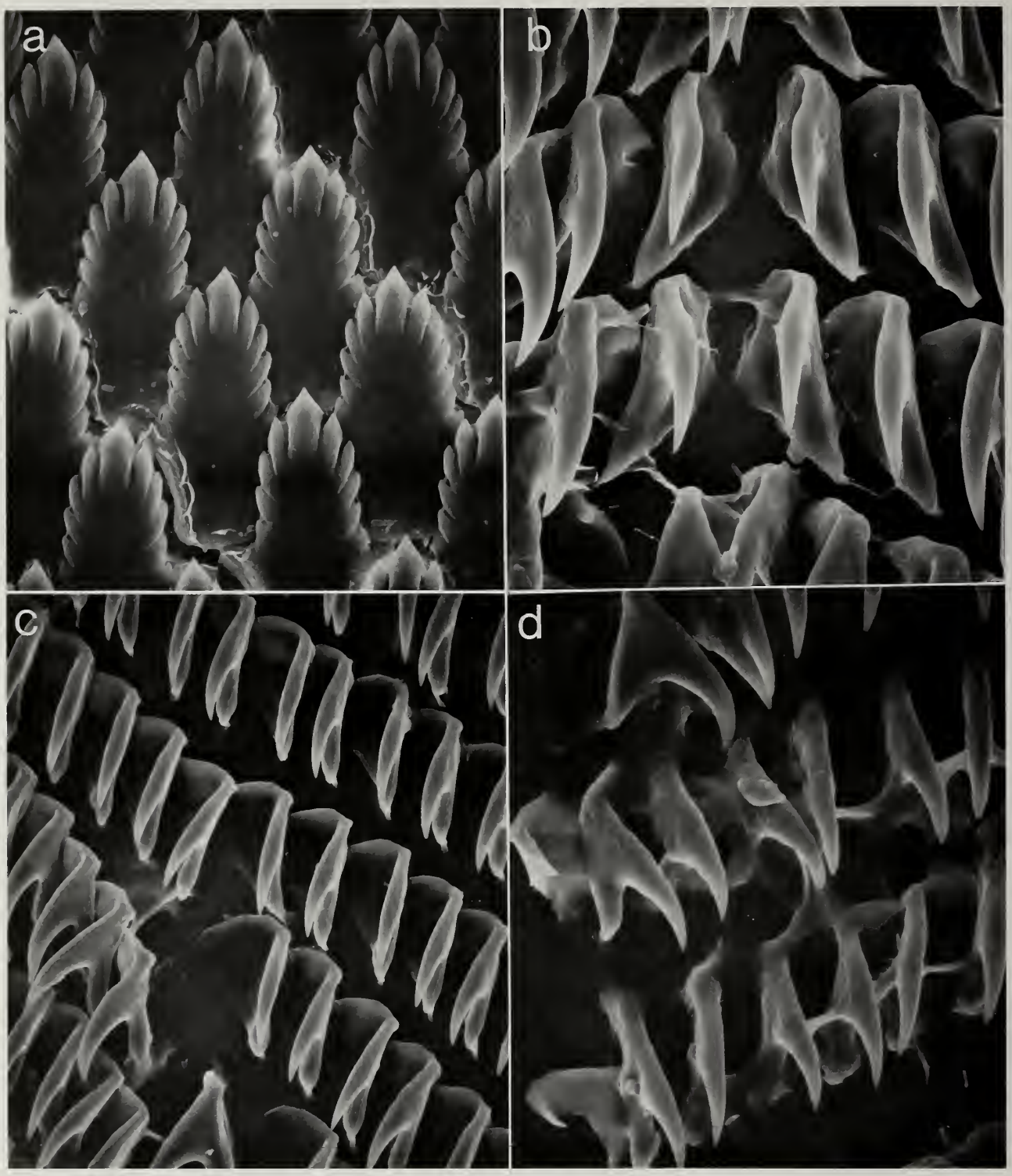

Figure 16

Berthella agassizii (MacFarland, 1909). Scanning electron micrographs of paratype. A. Jaw elements, ×2000. B. Inner lateral radular teeth, ×1300. C. Middle lateral radular teeth, ×800. D. Outer lateral teeth, ×1100.

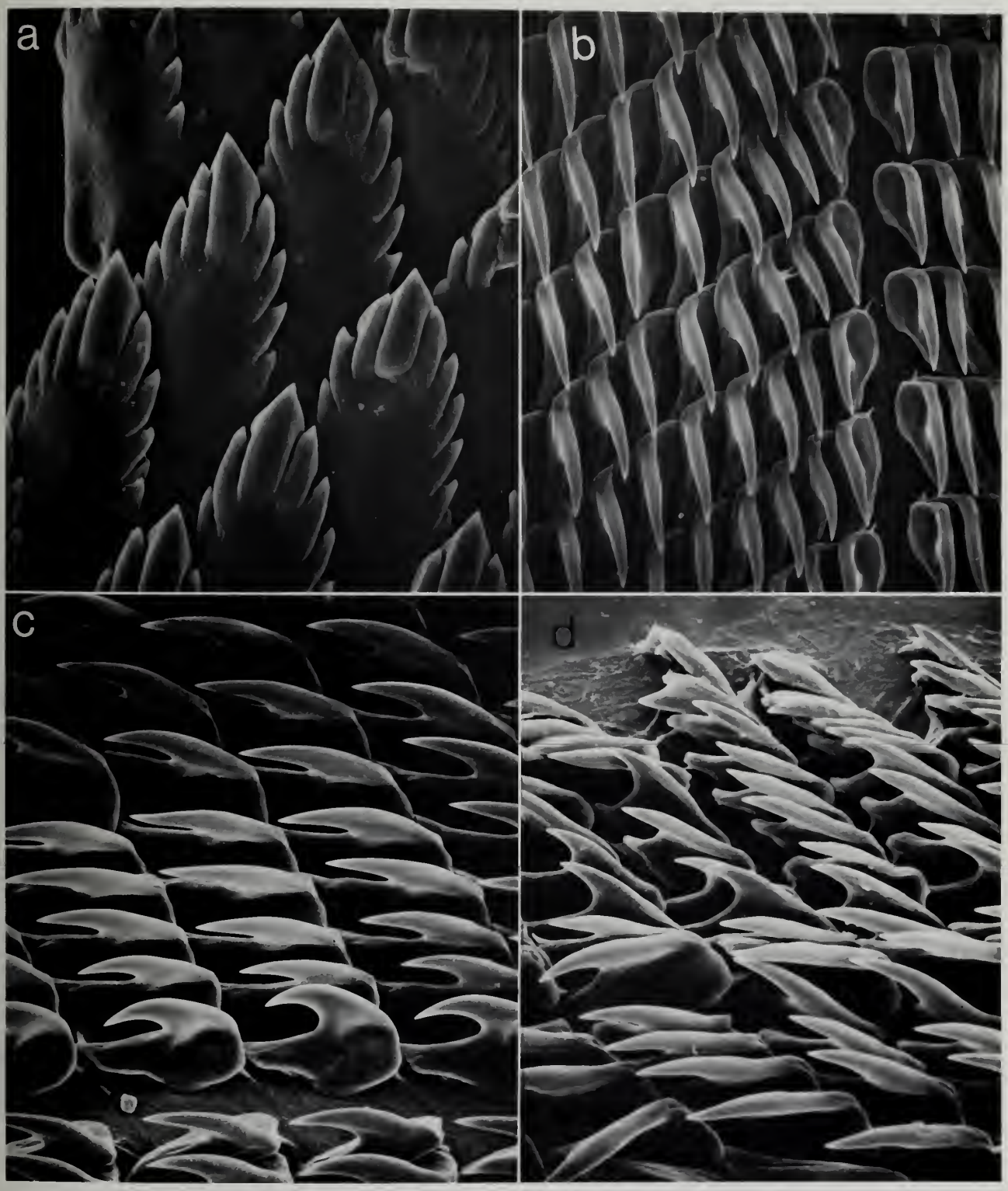

Figure 17

Berthella agassizii (MacFarland, 1909). Scanning electron micrographs of specimen from Campitos, Pacific coast of Baja California Sur, Mexico. A. Jaw, ×2000. B. Dorsal view of inner lateral teeth, ×800. C. Lateral view of inner lateral teeth, ×1200. Outer lateral teeth, ×1280.

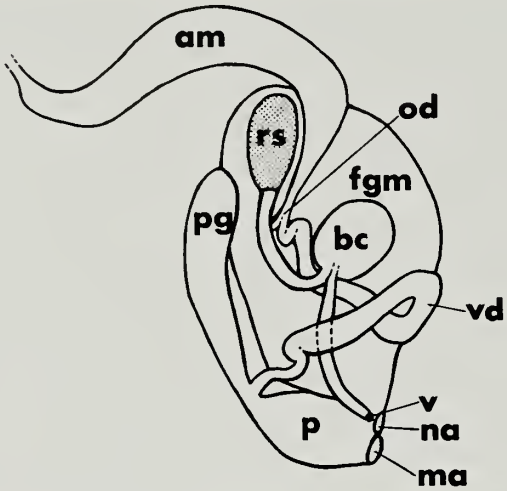

Figure 18

Berthella agassizii (MacFarland, 1909). Reproductive system of specimen from Campitos, Baja California Sur, Pacific coast of Mexico: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; ma, male aperture; na, nidamental aperture; od, oviduct; p, penis; pg, penial gland; rs, receptaculum seminis; v, vagina; vd, vas deferens.

with the penial gland. The penial gland is slightly curved, but not convoluted. The penial papilla is short and conical within a bulbous male atrium. In all four specimens examined, one each from both coasts of Baja California (present study), the paratype of *Berthella agassizii* from Brazil (present study) and from an unspecified locality in the Caribbean (Ev. Marcus, 1984, as *B. agassizii*), the receptaculum seminis contains black pigment internally. Even in MacFarland's specimen, collected in 1899, traces of pigment are still present in the receptaculum. The duct of the receptaculum joins the vagina either at the base of the spherical bursa copulatrix or in the middle of the vaginal duct.

Discussion: *Berthella agassizii* is sympatric with the circumtropical *B. stellata* within the Caribbean (Ev. Marcus, 1984) and along both coasts of Baja California (present study).

The two species differ consistently in several aspects of their external and internal morphology. *Berthella agassizii* has a reddish or pink notum, while that of *B. stellata* is translucent white or honey colored. The opaque white markings of *B. agassizii* are small spots and never form the broad crosses characteristic of *B. stellata*. In *B. agassizii*, the anus is situated near the middle of the gill membrane, while in *B. stellata* it is at the posterior limit of the gill.

The radular teeth of *Berthella agassizii* are uniformly hook-shaped, while in *B. stellata* the outermost teeth are elongate with a secondary denticle.

The reproductive system of *Berthella agassizii* differs from that of *B. stellata* in two significant regards. In *B. agassizii* the receptaculum seminis contains dark pigment, while that of *B. stellata* is unpigmented. In *B. agassizii* the penial sac is proportionally larger than in *B. stellata*.

DISCUSSION

Until recently, generic differences within the notaspideans have long been the source of considerable confusion. Much of this confusion stems from the fact that many external characters, such as the relative proportions of the mantle and foot, have been shown to be artifacts of preservation (Ev. Marcus & Gosliner, 1984; Willan, 1984). Also, the shape of jaw elements and radular teeth varies within a population, or even within a single individual.

There has been considerable confusion surrounding the separation of *Pleurobranchus* from *Berthella*. *Pleurobranchus* had been separated from *Berthella* by its tuberculate ctenidium and by having a diaulic rather than triaulic arrangement of reproductive organs.

Recently, Willan (1987) has revised the notaspidean genera, based on a cladistic analysis of morphological characters. He demonstrated that gill tuberculation and diauly versus triauly are useful in separating *Pleurobranchus* from *Berthella*. He also noted additional characters that are useful in separating *Berthella, Bathyberthella, Berthellina,* and *Pleurehdera* (tribe Berthellini) from their sister taxon, *Pleurobranchus*. Living *Pleurobranchus* pulsate the rhinophores. This may be an adaptation for increasing respiration in these large, active animals. Members of *Pleurobranchus* also have prominent flaps surrounding the genital apertures.

It should be noted that the triaulic arrangement of reproductive ducts present in the genera *Berthella, Pleurehdera, Bathyberthella,* and *Berthellina* is fundamentally different from that of doridacean nudibranchs. In dorids, the uterine duct connects the receptaculum seminis and bursa copulatrix with the female gland mass. In these triaulic notaspideans, a uterine duct is absent and the only connection of the receptaculum and bursa with the female gland mass is at the common genital atrium.

The genus *Pleurehdera* Marcus & Marcus, 1970b, was established to accommodate *P. haraldi* Marcus & Marcus, 1970b. It differs from *Berthella* by having bifid radular teeth. Willan (1987) noted that it is the most poorly differentiated notaspidean genus and suggested that it is allied to *Berthellina*. The fact that the presence of bifid teeth may vary within a single species (*Berthella stellata*, present study) indicates that this character, alone, cannot be used for generic separation. Willan (1987) noted that the shell of *Pleurehdera* is larger than that present in *Berthellina*, and is therefore more similar to the shell of *Berthella*. *Berthellina* also possesses elongate radular teeth with multiple denticles along their length. The radular teeth of *Pleurehdera haraldi* (Willan, 1984:fig. 1) are virtually identical to those seen in some specimens of *Berthella stellata* (Figure 11). On this basis, further study of *Pleurehdera* must be undertaken to re-examine its systematic placement and relationship to *Berthella* and *Berthellina*. Although considerable morphological variability has been previously

reported within the Pleurobranchidae, we have found that two widespread species, *Berthella stellata* and *B. martensi*, are among the most variable species of notaspideans. Much of the range of variation is present within single populations of these species.

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LITERATURE CITED

Behrens, D. W. 1980. Pacific coast nudibranchs, a guide to the opisthobranchs of the northeastern Pacific. Sea Challengers: Los Osos. 112 pp.

Bergh, R. L. S. 1898. Die Pleurobranchiden—*Pleurobranchus*. *In:* C. Semper (ed.), Reisen im Archipel der Philippinen von Dr. C. Semper. Malacol. Unter. 9(2)5–8:57–115.

Bertsch, H. 1975. Distributional and anatomical observations of *Berthella tupala* (Opisthobranchia: Notaspidea). Nautilus 89(4):124–126.

Burch, J. Q. 1944. Minutes of the Conchological Club of Southern California 37:17–18.

Burn, R. 1962. On the new pleurobranch subfamily Berthellinae (Mollusca: Gastropoda); a revision and new classification of the species of New South Wales and Victoria. Mem. Natl. Mus. Victoria 25:129–148.

Dall, W. H. 1900. A new species of *Pleurobranchus* from California. Nautilus 14(8):92–93.

Engel, H. 1927. Westindische opisthobranchiate Mollusken. II. Aplysiidae. Bijdr. Dierk. Aflever. 25:83–122.

Gosliner, T. 1987. Nudibranchs of southern Africa, a guide to opisthobranch molluscs of southern Africa. Sea Challengers and Jeff Hamann: Monterey. 136 pp.

Heller, J. & T. E. Thompson. 1983. Opisthobranch molluscs of the Sudanese Red Sea. Zool. Jour. Linn. Soc. 78:317–348.

Kay, E. A. 1979. Hawaiian marine shells. Reef and shore fauna of Hawaii. 4. Mollusca. Bernice P. Bishop Mus. Spec. Publ. 64(4):1–653.

Lance, J. R. 1966. New distributional records of some northeastern Pacific Opisthobranchiata with descriptions of two new species. Veliger 9(1):69–81.

Lee, R. S. & N. Foster. 1985. A distributional list with range extensions of the opisthobranch gastropods of Alaska. Veliger 27(4):440–448.

MacFarland, F. M. 1909. The opisthobranchiate Mollusca of the Branner-Agassiz Expedition to Brazil. Leland Stanford Jr. Univ. Publ. 2:1–104.

MacFarland, F. M. 1966. Studies of opisthobranchiate mollusks of the Pacific coast of North America. Mem. Calif. Acad. Sci. 6:1–546.

Marcus, Er. 1955. Opisthobranchia from Brazil. Bolm. Fac. Fil. Cien. Let. Univ. S. Paulo Zool. 18:165–203.

Marcus, Er. 1957. On Opisthobranchia from Brazil. (2). Jour. Linn. Soc., Zool. 43(292):390–486.

Marcus, Er. & Ev. Marcus. 1967. American opisthobranch mollusks. Stud. Trop. Oceanogr. Miami 6:1–256.

Marcus, Er. & Ev. Marcus. 1970a. Opisthobranchs from Curaçao and faunistically related regions. Stud. Fauna Curaçao 59:1–129.

Marcus, Er. & Ev. Marcus. 1970b. Opisthobranch mollusks from the southern tropical Pacific. Pac. Sci. 24(2):155–179.

Marcus, Ev. 1984. The western Atlantic warm water Notaspidea (Gastropoda, Opisthobranchia). 2. Bolm. Zool. Univ. S. Paulo 8:43–76.

Marcus, Ev. & T. Gosliner. 1984. Review of the family Pleurobranchaeidae (Mollusca: Opisthobranchia). Ann. S. Afr. Mus. 93(1):1–52.

Martens, E. von. 1880. Mollusken. Pp. 179–352. *In:* K. A. Möbius (ed.), Beiträge zur Meeresfauna der Insel Mauritius und der Seychellen, bearbeitet nach Sammlungen angelegt auf einer Reise nach Mauritius von K. Moebius. Guttmann Buchhandlung: Berlin. 352 pp.

Pease, W. H. 1860. Descriptions of new species of Mollusca from Sandwich Islands. Proc. Zool. Soc. Lond. 28:18–37.

Pilsbry, H. A. 1896. Manual of conchology 16:1–262.

Pruvot-Fol, A. 1954. Mollusques opisthobranches. Faune de France 58:1–460.

Risbec, J. 1928. Études anatomiques des gastéropodes tectibranches de la presqu'ile de Noumea. Arch. Mus. Hist. Nat., Ser. 6, 3:37–68.

Risso, A. 1826. Histoire naturelle des principales productions de l'Europe méridionale et particulièrement des celles des enviorns de Nice et des Alpes maritimes. 4:1–439.

Roller, R. A. 1970. A list of recommended nomenclatural changes for MacFarland's "Studies of opisthobranchiate mollusks of the Pacific coast of North America." Veliger 12(3):371–374.

Sphon, G. 1972. *Berthella kaniae*, a new opisthobranch from the eastern Pacific. Nautilus 86:53–55.

Thompson, T. E. 1970. Eastern Australian Pleurobranchomorpha (Gastropoda, Opisthobranchia). Jour. Zool. (Lond.) 160:173–198.

Thompson, T. E. 1981. Taxonomy of three misunderstood opisthobranchs from the northern Adriatic Sea. Jour. Moll. Stud. 47(1):73–79.

Thompson, T. E. 1985. Aposematic colour patterns of two Mediterranean species of opisthobranch molluscs: a proposal for co-operative investigation. Jour. Moll. Stud. 51:222–226.

Vayssière, A. 1896. Description des coquilles de quelques espèces nouvelles ou peu connues de pleurobranchidés. Jour. Conchyliol. 44:113–137.

Willan, R. C. 1984. The Pleurobranchidae (Opisthobranchia: Notaspidea) of the Marshall Islands, central-west Pacific Ocean. Veliger 27(1):37–53.

Willan, R. C. 1987. Phylogenetic systematics of the Notaspidea (Opisthobranchia) with reappraisal of families and genera. Amer. Malacol. Bull. 5(2):215–242.

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Two New Species of *Plocamopherus* from the Western Warm Water Atlantic

by

JEFFREY C. HAMANN

475 W. Bradley Avenue, El Cajon, California 92020, U.S.A.

AND

WESLEY M. FARMER

3591 Ruffin Road, No. 226, San Diego, California 92123, U.S.A.

Abstract. Two new species of *Plocamopherus* (Mollusca: Gastropoda: Opisthobranchia) from the western warm water Atlantic are described and their unique features are discussed. *Plocamopherus gulo* Marcus, 1979, is reascribed to the genus *Kaloplocamus* Bergh, 1892.

INTRODUCTION

There are presently 14 species of *Plocamopherus* described from tropical and subtropical waters. THOMPSON (1975) proposed recognizing only six of these species and certainly some will prove to be indistinct with further study. Only one, *Plocamopherus maderae* (Lowe, 1842), is reported from the warm water Atlantic. Two new Atlantic species are discussed in the following description representing a significant addition to a sparsely represented and poorly documented genus.

Family POLYCERIDAE Thiele, 1931

Genus *Plocamopherus* Rüppell & Leuckart, 1831

Plocamopherus ***lucayensis*** Hamann & Farmer, sp. nov.

(Figures 1–6)

Etymology: The area in which this species was collected was at one time occupied by the Lucayan Indians. The names of many local landmarks refer to this heritage and it was for this reason the name ***lucayensis*** was chosen.

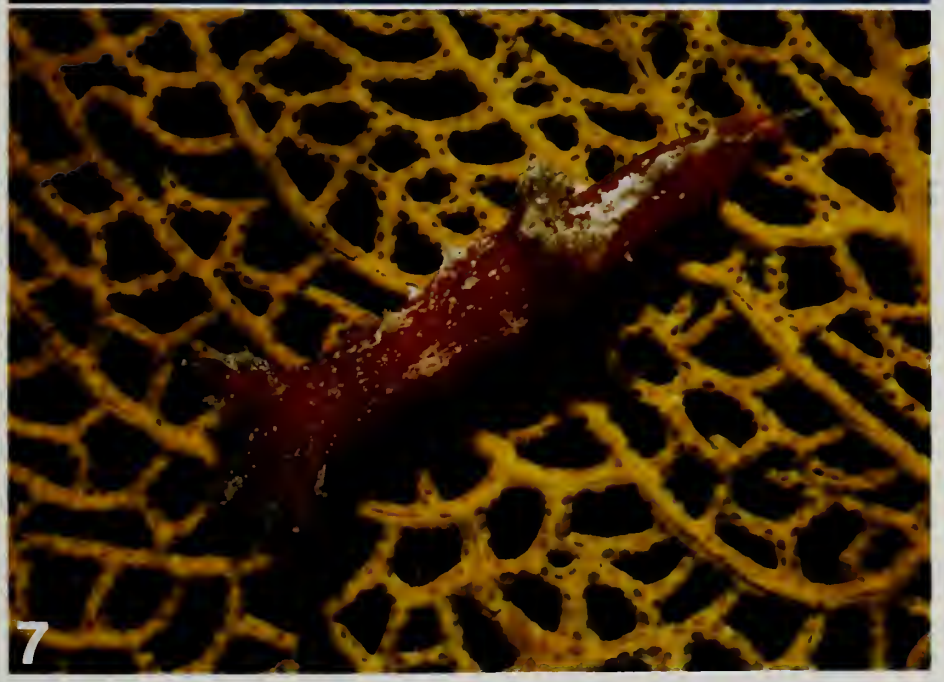
Material examined: Eight specimens were collected by Jack Worsfold in June 1984. The living animals were up to 40 mm long and were found feeding on a bryozoan of the family Bugulidae. The brown bryozoan colonies hung in loose spirals up to 75 cm long. The specimens were found on the underside of floating boat docks in the Bell Channel Canal, 0.5 mile (0.8 km) east of the Bell Channel entrance, Grand Bahama, Bahamas (26°31′40″N, 78°37′60″W).

Holotype: (1) One specimen (16 mm long preserved) is deposited in the collection of the California Academy of Sciences, Department of Invertebrate Zoology, San Francisco, California, CAS 064679. A color transparency and a sample of the bryozoan prey (CAS 064679) are on file with the holotype.

Paratypes: (2) One specimen (12 mm preserved) is deposited in the CAS collection, CAS 064677. (3) One specimen (9 mm preserved) is deposited in the CAS collection, CAS 064678. (4) One mounted radula is deposited in the CAS collection, CAS 064710. (5) One specimen (16 mm preserved) is deposited in the National Museum of Natural History, USNM 859307. (6) One specimen (10 mm preserved) is deposited in the National Museum of Natural History, USNM 859308.

Description: The body is a uniform reddish orange (Mars Orange from lefranc & bourgeois color chart) with white-tipped, tapering papillae of various sizes placed randomly over the entire dorsal surface. The tips are translucent white (Figure 1).

Most of the papillae bear a dark brown subapical band. They occur at a rate of approximately 124 per cm^2 on a 40-mm specimen with a decrease in density approaching the edge of the foot. The largest papillae are 1 mm long and 0.3 mm in diameter at the base, but most are considerably smaller.



Explanation of Figures 1 and 7

Figure 1. *Plocamopherus* ***lucayensis*** Hamann & Farmer, sp. nov. Photograph by Jack Worsfold.

Figure 7. *Plocamopherus* ***pilatecta*** Hamann & Farmer, sp. nov. Photograph by Jeff Hamann.

The general body shape is long and cylindrical, tapering to a blunt tail. Midway between the rhinophores and the branchial plume, the body is 7 mm wide by 7 mm high in a 40-mm specimen. There is no hint of a notal rim (Figure 2).

The foot has a thin edge that projects laterally approximately 1 mm. The anterior border of the foot is bilabiate and the corners form two enrolled propodial tentacles. The tentacles end in a blunt point 2–3 mm from the foot (Figure 3). They are the same Mars Orange color as the body and

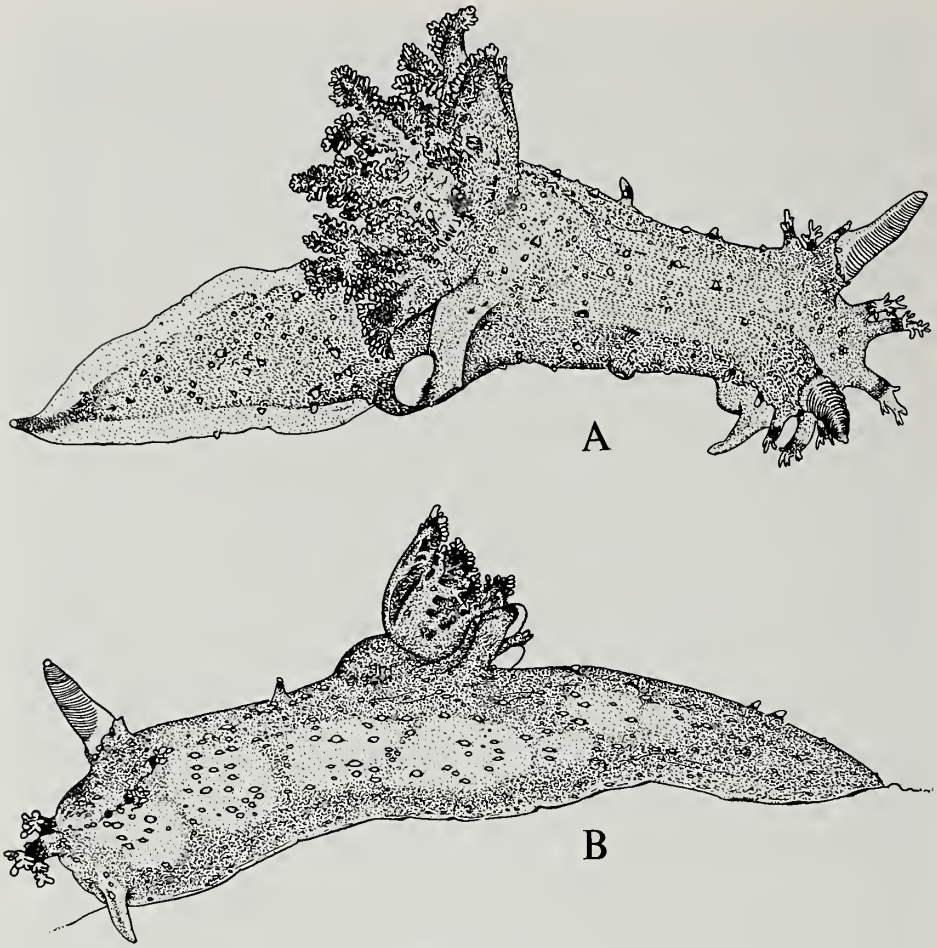


Figure 2

Plocamopherus ***lucayensis*** sp. nov. A. Right dorso-lateral view. B. Left lateral view. Length 40 mm.

are visible from most anterior angles. The tail tapers to a blunt point and has a dark brown ridge.

The frontal veil bears 8–10 unevenly spaced processes up to 2 mm long. The distal one-third of each process is translucent white and irregularly branched. The white tips are followed by a poorly defined dark brown band as in the dorsal papillae.

The finely lamellate rhinophores have 33 lamellae that closely approach the rhinophoral sheath. The rhinophores are orange with increasing dark brown shading approaching a minute white tip. The clavus tapers evenly from 2 mm at the base to a blunt tip and is 5 mm long on a 40-mm specimen. The rhinophoral sheaths are rimmed in dark brown and lined with papillae following the same color pattern as the dorsal papillae.

The large branchial plume has 6 or 7 bipinnate and tripinnate gills, the anterior 3 being slightly larger. The same Mars Orange color covers all but the very ends of the gills, which shade into dark brown with translucent white tips. The six gills are arranged in a horseshoe around the anus (Figure 4). One 1.5 mm wide by 6 mm long extrabranchial appendage is fixed just under the gills on each side about two-thirds of the way back from the anterior gill. The distal one-third of these cylindrical processes consists of an opaque white hemisphere that is directed posteriorly. This 2-mm bulb is very prominent and ringed with dark brown.

Although many species of *Plocamopherus* are reported to have light-emitting and swimming capabilities, neither behavior was observed in this species.

Radula: The radula is long and narrow with a bare rachis. The radular formula is 9 × 3·2·0·2·3. The two inner laterals are distinctive hooks, while the three remaining outer laterals are simple blades. The first lateral tooth has a wide base and the second has a small point on top of the hook (Figure 5). The radula is dark amber in color. The jaw plates are clear and roughly triangular in shape with a smooth texture.

Reproductive system: The genital pore is located on the right side of the body one-half of the way from the rhinophore to the extrabranchial appendage and 2 mm below a line drawn between the two.

The reproductive system (Figure 6) is triaulic and the

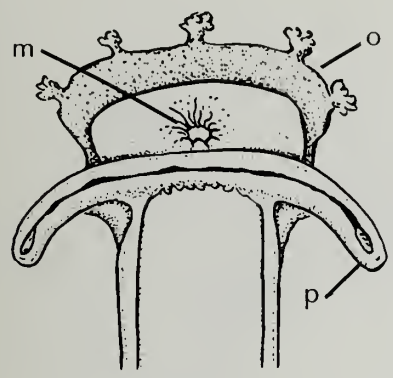


Figure 3

Ventral view of head region of *Plocamopherus* ***lucayensis***. m, mouth; o, oral veil; p, propodial tentacles.

penis is armed with many small spines. In the penial sheath there are pointed fleshy papillae. The non-prostatic portion of the vas deferens is long and convoluted. The prostatic portion envelops the bursa copulatrix with coils of flat tubes. The bursa copulatrix is smooth and spherical.

The female reproductive system is serially arranged following the terminology of ODHNER (1926). The vagina is smooth and thin walled. It inflates slightly and turns before narrowing to enter the bursa copulatrix. The distal vaginal duct emerges from the bursa copulatrix at some distance from the entrance of the vagina. It traverses a distance equal to the length of the bursa copulatrix and then enters the receptaculum seminis. The short uterine duct connects the receptaculum seminis to the female gland mass.

Plocamopherus ***pilatecta***
Hamann & Farmer, sp. nov.

(Figures 7–12)

Etymology: The specific name chosen for this *Plocamopherus* is a compound of the Latin words *pila,* meaning "ball," and *tecta,* meaning "covered." One of the characteristics of this genus is the extrabranchial appendages, which terminate in a globular structure. These appendages are almost completely hidden by accompanying arborescent processes and the branchial plume in this species.

Material examined: Three specimens were examined altogether. Two specimens were collected by Gregg Hamann in the Grenadines of St. Vincent, West Indies, in March

Figure 4

Schematic drawing of gill arrangement around anus in *Plocamopherus* ***lucayensis***.

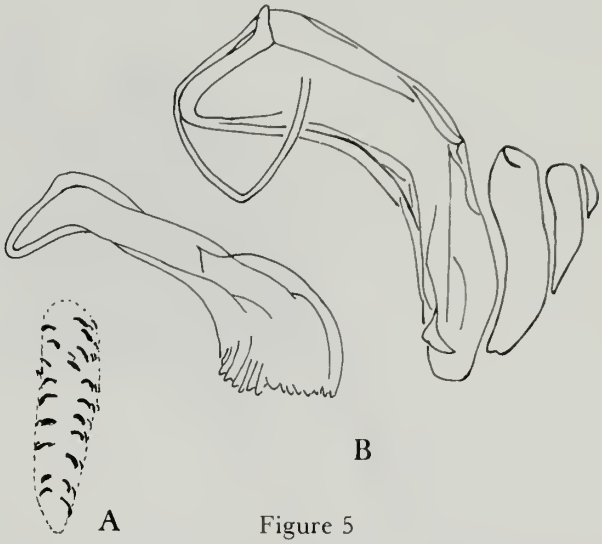


Figure 5

Radula of *Plocamopherus* ***lucayensis***. A. Schematic drawing showing shape of radula. B. Half row of teeth.

of 1987. The third specimen was collected by Jeff Hamann on Guadeloupe, West Indies, in January 1986.

Holotype: (1) One specimen approximately 28 mm long alive (17 mm preserved) is deposited in the collection of the California Academy of Sciences, Department of Invertebrate Zoology, San Francisco, California, CAS 064680. The specimen was collected at Princess Margaret Beach, Bequia, Grenadines of St. Vincent (12°59′40″N, 61°15′14″W). It was found at night in 21 m of water feeding on the bryozoan *Zoobotryon vericillatum* Delle Chiage.

Paratypes: (2) The second specimen, collected with the holotype and measuring approximately 24 mm alive (15 mm preserved), is also deposited in the CAS collection, CAS 064681. (3) The third specimen (12.5 mm live, 6

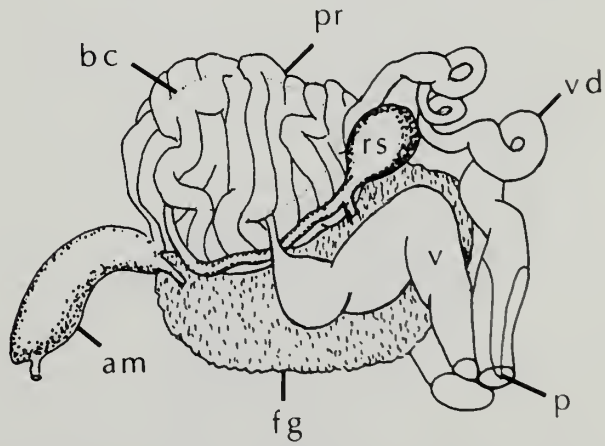


Figure 6

Reproductive system of *Plocamopherus* ***lucayensis***. am, ampulla; bc, bursa copulatrix; fg, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; v, vagina; vd, vas deferens.

Figure 8

Plocamopherus ***pilatecta*** sp. nov. Right dorso-lateral view. Length 12.5 mm.

mm preserved) was collected in 20 m of water between Pt. Botrel and Pt. Mahout on the west coast of Guadeloupe, West Indies (16°11′N, 61°47′50″W). The bottom was muddy owing to a nearby river mouth and the specimen was found at night feeding on *Zoobotryon vericillatum*. This partially dissected specimen, along with its mounted radula, is deposited in the collection of the National Museum of Natural History, Washington, D.C., USNM 859309.

Description: The three specimens examined varied in color from yellow to yellow-ochre to orange. A creamy white irregular band runs around the frontal veil, along the notal ridges, and down the ridge of the tail. A frosting of the same color occurs on the dorsum and the sides of the body. Four or five white papillae occur on each side in a line midway between the notal rim and the edge of the foot. The entire animal is translucent enough to see vague interior features. Two eye spots are visible 2 mm behind the rhinophores and 1 mm apart (Figure 7).

The general body form is long and cylindrical. The 12.5-mm specimen was 3 mm wide and 3 mm high midway from the rhinophores to the branchiae. The notal rim has three pairs of arborescent processes up to 2 mm long. Two pairs occur between the branchiae and the rhinophores and one pair occurs behind the branchiae at the posterior notal corners. They are creamy white like the notal bands. The posterior pair is accompanied by cylindrical processes typical of the genus. These well-hidden extrabranchial appendages are 2 mm in diameter and 4 mm long in a 27-mm specimen with a pink or white hemisphere on the end. Rudiments of additional processes are apparent on the dorsal ridge running down the tail (Figure 8).

The frontal veil on the 27-mm specimen has 7 or 8 larger arborescent processes and many smaller ones. Fully expanded, the frontal veil is 9 mm wide on a 27-mm specimen. The oral tentacles are triangular and pointed laterally (Figure 9).

The white-tipped rhinophores are the same color as the body and are dusted with white and brown in varying amounts. They have 11 or 12 lamellae. The bare stalk is about the same length as the lamellate portion of the rhinophore.

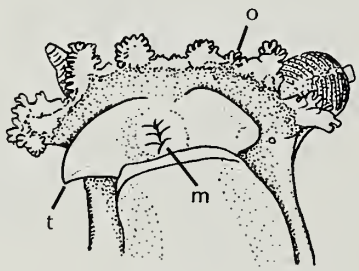


Figure 9

Ventral view of head region of *Plocamopherus* ***pilatecta***. m, mouth; o, oral veil; t, oral tentacles.

Figure 10

Schematic drawing of gill arrangement around anus of *Plocamopherus* ***pilatecta***.

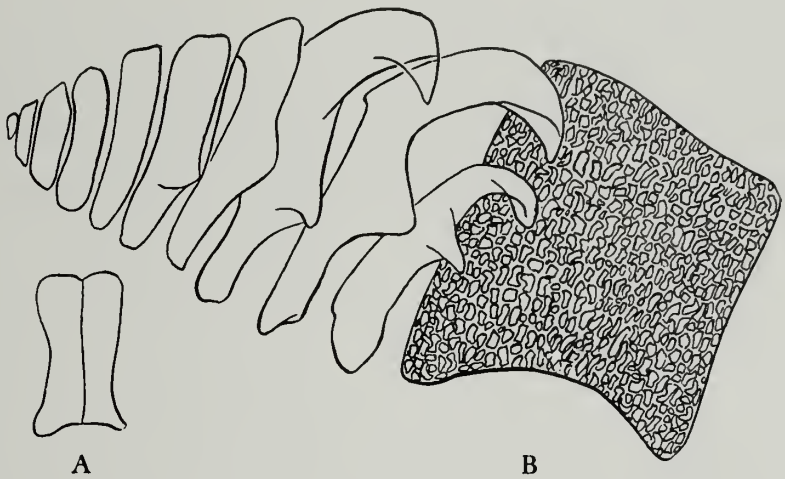


Figure 11

Radula of *Plocamopherus* ***pilatecta***. A. Schematic drawing showing shape of radula. B. Half row of teeth, and granulated rachis.

The branchial plume is composed of three finely branched, tripinnate gills wrapped around the anus (Figure 10). They are creamy white like the frontal veil and notal ridge.

The foot is rounded anteriorly and sharply pointed posteriorly. It is colored a uniform light orange or yellow. A thin edge of the foot extends laterally 1 mm on a 27-mm specimen.

The animal swims in a lateral head to tail motion. It flattens its tail vertically while swimming. When disturbed, the white portions of the body emit a green-white light visible in daylight shadows. This response was observed only twice in the course of a week's captivity. Light organs are not uncommon in *Plocamopherus* and have been reported in *P. imperialis* Angas, 1864, by Willan & Coleman (1984), in *P. tilesii* Bergh, 1877, by Bertsch & Johnson (1981), and in *P. maderae* (Lowe, 1842) by Risbec (1928). The luminous organ in *P. tilesii* is discussed in detail by Okada & Baba (1938).

Radula: The narrow radula has a formula of 12 × 7·3·0·3·7 in a 12.5-mm specimen and 16 × 10·4·0·4·10 in a 24-mm specimen. The bare rachis is wide with a granulated membrane. The inner lateral teeth of each row are hook-shaped with a low cusp on the shank. The next two or three lateral teeth are flat blades with a similar low cusp on the shank. The remaining five to seven teeth are simple blades (Figure 11). The jaw plates are roughly triangular and yellow.

Reproductive system: The penis is surrounded by a heavily muscled penial duct. There is a large inflation on the vas deferens before it narrows and enters the tightly coiled prostatic portion.

The female reproductive system is serially arranged following the terminology of Odhner (1926). The vagina makes two turns before widening into a long section with longitudinal striations. From there, it narrows and enters the spherical bursa copulatrix. The distal vaginal duct exits the bursa copulatrix near the vaginal duct and after a long smooth section branches off to the receptaculum seminis. The shorter, convoluted uterine duct continues on to the female gland mass (Figure 12).

Discussion: *Plocamopherus* Rüppell & Leuckart, 1831, belongs to the family Polyceridae Theile, 1931. Risbec (1928) united *Triopha* Bergh, 1880, with *Plocamopherus* but the synonymy has largely been rejected among subsequent workers. *Plocamopherus* is differentiated from *Triopha* by the presence of club-shaped extrabranchial appendages (Ferreira, 1977). Eliot (1906) characterized *Plocamopherus* as having branched processes on the oral veil and dorsal margin, flat ridge-like oral tentacles, a bare

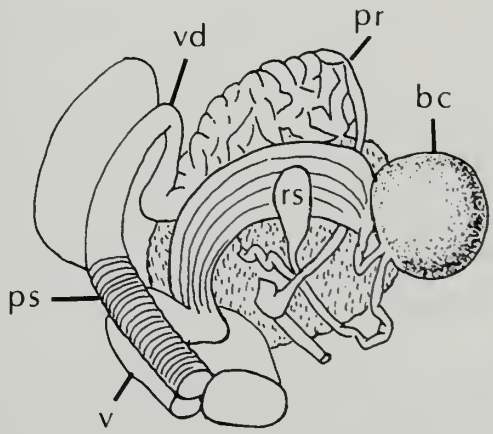


Figure 12

Reproductive system of *Plocamopherus* ***pilatecta***. bc, bursa copulatrix; pr, prostate; ps, penial sheath; rs, receptaculum seminis; v, vagina; vd, vas deferens.

wide rachis of the radula, 3–11 inner hamate teeth, flat plates for outer teeth, and a dendritic prostate enveloping the spermatotheca. PRUVOT-FOL (1954) added that most species have clublike or spherical processes that are light-emitting. RISBEC (1953) identified a voluminous prostate and armed penis as being representative of the genus.

THOMPSON (1975) briefly reviewed the genus and listed six valid species. MARCUS (1979) listed 14 species of *Plocamopherus* and described a new species. *Plocamopherus gulo* Marcus, 1979, fits into the genus *Plocamopherus* in most respects but lacks the clublike or spherical extra-branchial appendages and should be placed in the genus *Kaloplocamus* Bergh, 1892. *Kaloplocamus* can be differentiated from *Triopha* by the presence of branched notal processes, versus simple processes in *Triopha*.

Although *Plocamopherus* ***lucayensis*** resembles the 14 presently described species of *Plocamopherus* in general body form it can be differentiated by the following characteristics: (1) None shares a total lack of notal rim and notal processes. (2) Only *P. tilesii* Bergh, 1877, is recorded as sharing brown or amber radula. (3) *P. maderae* (Lowe, 1842), *P. tilesii* Bergh, 1877, *P. ceylonicus* (Kelaart, 1858), *P. maculatus* (Pease, 1860), *P. ocelatus* Rüppell & Leuckart, 1831, *P. imperialis* Angas, 1864, and *P. apheles* Barnard, 1927, are recorded as having a crested tail for swimming. *Plocamopherus* ***lucayensis*** has no hint of a crested tail. (4) No other *Plocamopherus* is recorded as having tentacular foot corners. (5) At 9 × 3·2·0·2·3, the radula of *P.* ***lucayensis*** is narrower than any of the other species. *Plocamopherus fulgurans* Risbec, 1928, is the closest at 25 × 7·3·0·3·7.

Plocamopherus ***pilatecta,*** on the other hand, is more typical of the genus, with flat oral tentacles, a crested tail, and well defined notal rim with processes. It most closely resembles the Atlantic species *P. maderae*. These two species can be differentiated by the following characteristics. (1) *P. maderae* has 15 large oral processes while *P.* ***pilatecta*** has 7 or 8 large processes. (2) *P. maderae* is red-orange with bright red, yellow, and brown spots while *P.* ***pilatecta*** is orange with cream-colored irregular frosting. (3) Both species have a wide bare radular rachis. In *P.* ***pilatecta*** the membrane of the rachis is granulated. In *P. maderae* it is divided by transverse lines connecting the teeth on each side. (5) The rhinophores in *P.* ***pilatecta*** are club-shaped with an equal plain shaft section and lamellate section, while the rhinophores in *P. maderae* are fully lamellate with no bare shaft. (6) Internally, the prostate envelops the bursa copulatrix in *P. maderae* but is separate in *P.* ***pilatecta***.

ACKNOWLEDGMENTS

We are grateful to Jack Worsfold for supplying the type material and photographs for *Plocamopherus* ***lucayensis***. His hospitality and enthusiasm were a continuing encouragement. We also thank Dave Behrens and Sandra Millen for reviewing the manuscript and Terry Gosliner for his expert help with the reproductive system dissections.

LITERATURE CITED

ANGAS, G. F. 1864. Description d'espèces nouvelles appartenant à plusieurs genres de mollusques nudibranches des environs de Port Jackson (Nouvelle-Galles du Sud), accompagnée de dessins faits d'après nature. Jour. Conchyl., Ser. 3, 12:43–70, pls. 4–6.

BARNARD, K. 1927. South African nudibranch Mollusca, with descriptions of new species, and a note on some specimens from Tristan da Cunha. Ann. S. Afr. Mus. 25(1):171–215, pls. 19, 20.

BERGH, L. S. R. 1877. Malacologische Untersuchungen. *In:* Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper. Zweiter Theil. Wissenschaftliche Resultate. Band 2, Theil 2, Heft 12, pp. 495–546.

BERGH, L. S. R. 1880. On the nudibranchiate gasteropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska. Proc. Acad. Natur. Sci. Phila. for 1880:40–127.

BERGH, L. S. R. 1892. Opisthobranches provenant des campagnes du yacht l'Hirondelle. Resultats des campagnes scientifiques accomplies sur son yacht (Hirondelle) par Albert 1 prince souverain de Monaco. No. 4:1–35.

BERTSCH, H. & S. JOHNSON. 1981. Hawaiian nudibranchs. Oriental Publishing Company: Honolulu, Hawaii. 112 pp.

ELIOT, C. 1906. Report upon a collection of Nudibranchiata from the Cape Verde, with notes by C. Crossland. Proc. Malacol. Soc. Lond. 7(3):131–159, pl. 14.

FERREIRA, A. J. 1977. A review of the genus *Triopha*. Veliger 19(4):387–402.

KELAART, E. F. 1858. Description of a new Ceylonese nudibranch. Ann. Mag. Natur. Hist., Ser. 3, 1(4):257–258.

LOWE, R. T. 1842. Description of a new dorsibranchiate gasteropod discovered at Madeira. Proc. Zool. Soc. Lond. 111: 51–53.

MARCUS, E. 1979. Campagne de la Calypso au large de côtes Atlantiques de l'Amerique du sud (1961–1962). Annales de l'Institut Océanographique, Monaco 55 (Suppl.):131–138.

ODHNER, N. H. 1926. Die Opisthobranchien. *In:* Further zoological results of the Swedish Antarctic Expedition 1901–1903 under the direction of Dr. Otto Nordenskjold 2(1):1–100.

OKADA, Y. & K. BABA. 1938. On the luminous organs of a nudibranch, *Plocamopherus tilesii* Bergh. Annot. Zool. Jap. 17(3, 4):276–281.

PEASE, W. H. 1860. Descriptions of new species of Mollusca from the Sandwich Islands. Proc. Zool. Soc. Lond. 28:18–37.

PRUVOT-FOL, A. 1954. Mollusques Opisthobranches. Faune de France, Paris 58:1–460.

RISBEC, J. 1928. Contribution à l'études des Nudibranches Néo-Calédoniens. Faune des Colonies Françaises 2(1):1–328.

RISBEC, J. 1953. Mollusques Nudibranches de la Nouvelle-Calédoniens. Faune Union Française Paris, Libraire Larose 15:1–189.

RÜPPELL, W. & F. LEUCKART. 1831. Mollusca. *In:* Atlas zu der Reise im nördlichen Afrika von Eduard Rüppell. Zool. Neue wirbellose Thiere des Rothen Meers. Pp. 15–47.

THIELE, J. 1931. Handbuch der Systematischen Weichtierkunde. A. Asher & Co.: Amsterdam. Band 1, vi + 778 pp. Reprinted 1963.

THOMPSON, T. E. 1975. Dorid nudibranchs from eastern Australia. Jour. Zool. 176(4):477–517.

WILLAN, R. C. & N. COLEMAN. 1984. Nudibranchs of Australasia. Australasian Marine Photographic Index, 103 Caringbah. N.S.W. Sydney, Australia. 56 pp.

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A New Species of Gymnosome, *Pneumodermopsis spoeli* (Gastropoda: Opisthobranchia), from the Great Barrier Reef, Australia

by

L. J. NEWMAN AND J. G. GREENWOOD

Zoology Department, University of Queensland, St. Lucia, Brisbane, Australia 4067

Abstract. Five specimens of a new gymnosome species, *Pneumodermopsis* ***spoeli***, were collected in zooplankton samples from waters of Australia's Great Barrier Reef, during 1984 and 1986. Specimens are illustrated and the new species is described. Amongst its unique features is the presence of only four suckers on a bifurcated median buccal arm. Morphological comparisons are made with three closely-related species: *Pneumodermopsis paucidens* (Boas, 1886) *s.s.*, *P. polycotyla* (Boas, 1886), and *P. teschi* van der Spoel, 1973.

INTRODUCTION

In 1984, an unusual specimen of *Pneumodermopsis* was collected off Lizard Island, northern Great Barrier Reef, Australia. Additional specimens were collected in 1986 from both Lizard and Heron islands, and the uniqueness of this new species was confirmed.

Pneumodermopsis species are rare within tropical and subtropical Australian waters. Of the 12 species known in the genus, four have been previously reported within Australian waters (VAN DER SPOEL, 1976; GREENWOOD & NEWMAN, 1985), these being *P. canephora* Pruvot-Fol, 1924, *P. macrochira* Meisenheimer, 1905, *P. paucidens* (Boas, 1886), and *P. simplex* (Boas, 1886).

The family Pneumodermatidae Pelseneer, 1887, is characterized by the presence of acetabuliferous (sucker-bearing) buccal arms that are only discernible when the buccal apparatus is extended. The number and arrangement of the suckers are species-specific. The genus *Pneumodermopsis* Keferstein, 1862, *sensu stricto* is characterized by having the following buccal structures: simple hook-sacs, lateral suckers attached to the buccal wall or on the lateral buccal arms, and a median acetabuliferous arm (VAN DER SPOEL, 1976). Previously known species have five suckers associated with the median arm, except for *P. teschi* which can show a reduction. These features are difficult if not impossible to observe in preserved specimens. We were able to observe the everted buccal apparatus in live individuals of the new species and of *P. paucidens* at research stations on the Great Barrier Reef (GBR). Comparisons with descriptions in the literature are difficult since previous authors did not report on some of the characteristic features, their specimens being preserved and contracted.

TAXONOMY

Pneumodermopsis ***spoeli***
Newman & Greenwood, sp. nov.

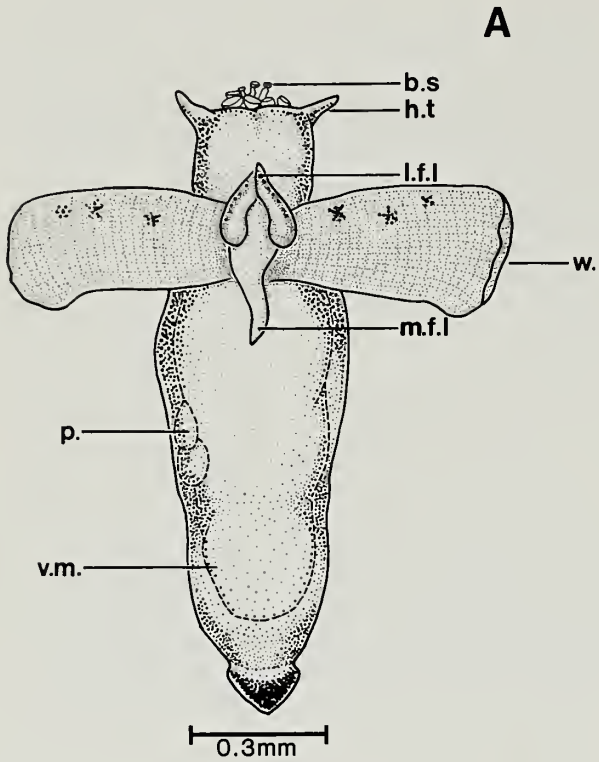
(Figures 1–3A, Table 1)

Methods: Five specimens of *Pneumodermopsis* ***spoeli*** were collected in zooplankton samples from waters of the Great Barrier Reef. Plankton tows were of 10-min duration with nets of 0.5-m diameter and mesh sizes of 0.5 and 0.2 mm. Depth of capture was 1–3 m below the surface.

All specimens were examined, photographed, and drawn while alive in the laboratory, then relaxed with magnesium sulphate and preserved in 5% buffered formalin for later examination of the radulae and hook-sacs. Radulae were dissected from the buccal cavity, left in 10% KOH for 24 h, and mounted for light microscopy. All material has been lodged with the Australian Museum, Sydney, Australia.

Materials: Holotype: The holotype was collected on 24 December 1984 off Watson's Bay, Lizard Island, northern GBR (14°40′S, 145°26′E) (AM C153114). Body length of the live animal was 2.65 mm.

Paratypes: One specimen was collected on 25 July 1986 off Casuarina Beach, Lizard Island, northern GBR (AM C153115). Live body length was 1.5 mm. Three specimens



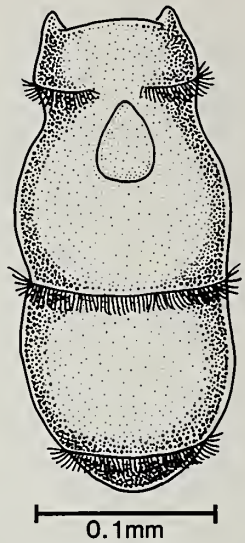
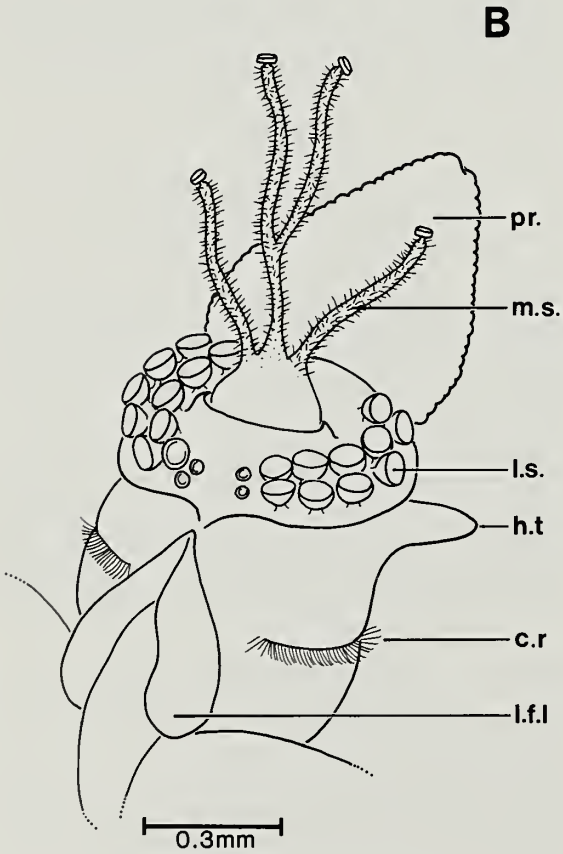


Figure 2

Polytrochous larvae of *Pneumodermopsis* ***spoeli***.



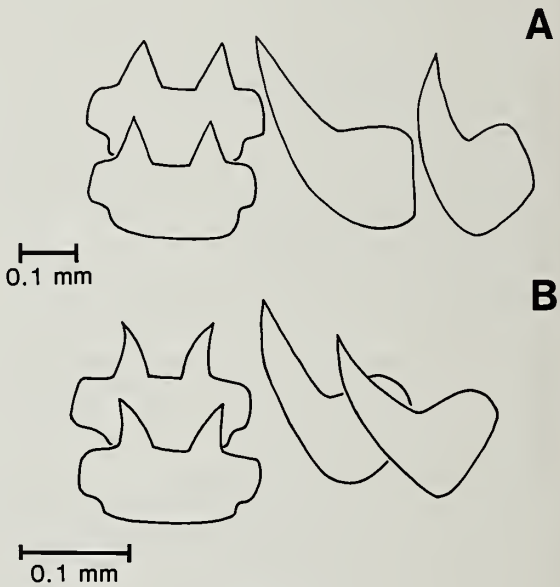


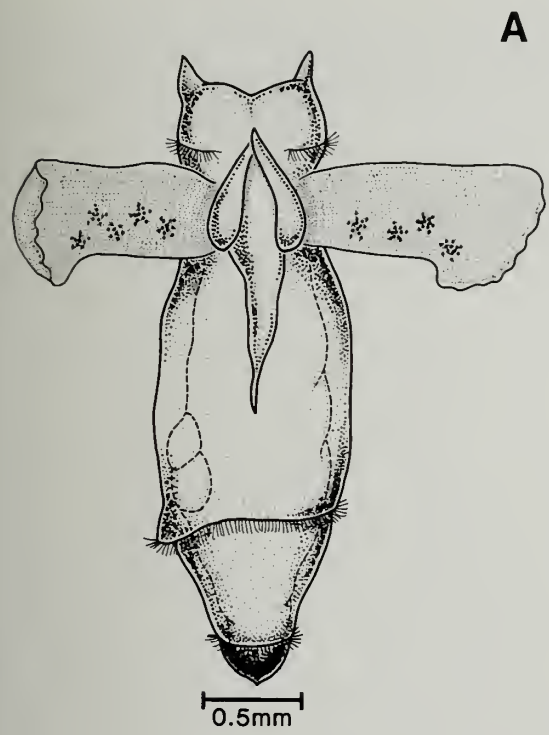
Figure 3

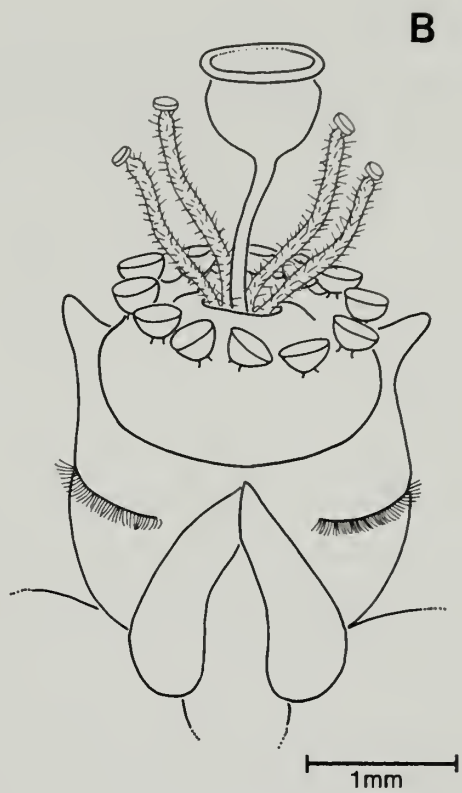
Radulae of *Pneumodermopsis* ***spoeli*** (A) and *P. paucidens* (B).

←

Figure 1

Pneumodermopsis ***spoeli***. A. Holotype, whole animal. B. Paratype, everted buccal apparatus. Abbreviations: b.s., buccal sucker; c.r., ciliary ring; h.t., head tentacle; l.f.l., lateral footlobe; l.s., lateral buccal sucker; m.f.l., median footlobe; m.s., median arm sucker; p., pericardium; pr., proboscis; v.m., visceral mass; w., wing.





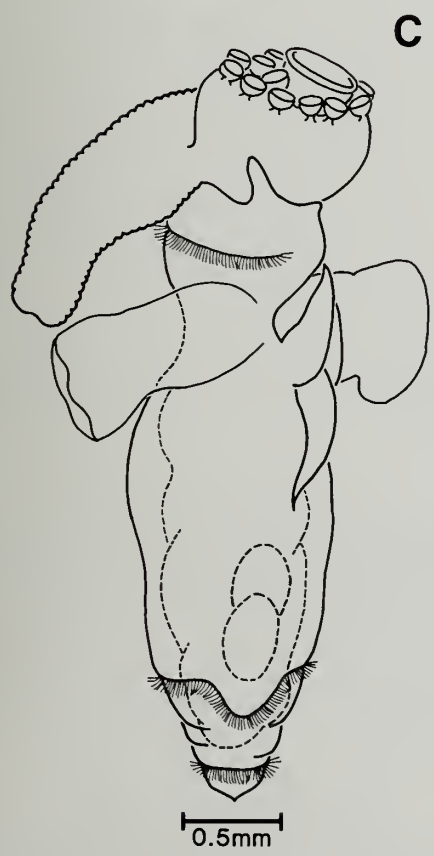


Figure 4

A. *Pneumodermopsis paucidens*, whole animal. B. Everted buccal apparatus. C. Lateral view of whole animal. Refer to Figure 1 for labels.

were collected from the channel between Heron and Wistari reefs, southern GBR (23°27′S, 151°55′E) on 8 September and 12 December 1986. Live body lengths were 1.1 mm (AM C153116), 1.0 mm (AM C153117), and 1.0 mm (AM C153118), respectively. Polytrochous larvae, assumed to be of this species, were collected from Heron Island in December 1986.

Description (Figures 1–3A, Table 1): The body is barrel-shaped when extended and rounded when contracted (Figure 1A). A posterior gill is present, but there is no lateral gill. Chromatophores are located on the head, trunk, and posterior region, and sparsely over the wings. The foot is composed of a long median lobe and two lateral lobes in close contact with each other. The internal organs, including the ovotestis, do not extend into the posterior region, terminating within two-thirds the length of the trunk.

The everted buccal wall displays 24 short, stalked suckers, with 12 suckers arranged in two parallel rows on each side of the median arm (Figure 1B). The more ventral two pairs of these suckers are small, being only half the size of the others. The median acetabuliferous arm is divided into three slender stalks, the center stalk being bifurcate. Each stalk or bifurcation is covered by fine hairlike projections and possesses a small sucker distally (Figure

Table 1

Comparisons of features of *Pneumodermopsis* ***spoeli***, *P. paucidens*, and *P. polycotyla* (data on *P. paucidens* and *P. polycotyla* derived from VAN DER SPOEL, 1976).

Species	Characters							
	Maximum length (mm)	Lateral gill	Posterior gill	Total no. lateral arm suckers	Total no. median arm suckers	Radula formula	No. hooks in hook-sac	Distribution
P. ***spoeli****, sp. nov.*	*2.65*	*absent*	*present*	*24*	*4*	*2·1·2*	*6*	*Great Barrier Reef, Australia*
P. paucidens (Boas, 1886)	5.0	present	present	10–12	5	2–3·1·2–3	5 or 6	Indo-Pacific, Atlantic, and Mediterranean
P. polycotyla (Boas, 1886)	5.0	present	?	20–24	5	3·1·3	10	off Chile
P. teschi van der Spoel, 1973	9.0	present	absent	12–20	3 or 5	3–7·1·3–7	9–35	NE Atlantic and Mediterranean

1B). The everted proboscis can extend to the same length as the body. The radula formula is 2·1·2, the median tooth being bicuspid (Figure 3A). There are six broadly triangular hooks in each hook-sac, the maximum hook height being 0.02 mm.

Remarks: *Pneumodermopsis* ***spoeli*** is unique within the genus in the median buccal arm having only four suckers, and having a bifurcated central stalk. In overall appearance *P.* ***spoeli*** closely resembles *P. paucidens* (Boas, 1886) *s.s.* (Figures 4A–C) and *P. polycotyla* (Boas, 1886). *Pneumodermopsis paucidens* was first recorded from Australian waters by GREENWOOD & NEWMAN (1985).

Pneumodermopsis paucidens differs from *P.* ***spoeli*** in having a lateral gill on the right side, and the visceral mass clearly extends to the posterior region (Figures 4A, C, Table 1). The buccal apparatus of *P. paucidens* also differs in that there are only 12 stalked suckers on the buccal wall (*cf.* 24 in *P.* ***spoeli***), and five median arm suckers (*cf.* 4); the medial sucker of the median arm is large, being at least three times the size of the buccal wall suckers (Figure 4B) (*cf.* absent in *P.* ***spoeli***). The proboscis, as shown from the lateral view (Figure 4C), is highly contractile and can extend the length of the body in both *P. paucidens* and *P.* ***spoeli***. In both species, fine hairlike projections are found on the median arm stalks. The radula formula of both species is 2·1·2, with a biscuspid central tooth. Curvature of these cusps differs slightly between the two species (Figure 3).

Pneumodermopsis polycotyla is also known from the southwestern Pacific but differs from *P.* ***spoeli*** in having a long lateral gill, five suckers on the median arm and a radula formula of 3·1·3 with a tricuspid central tooth (Table 1).

The only other species to show a reduction of median arm suckers is *Pneumodermopsis teschi*. This species differs from *P.* ***spoeli*** especially in having a well developed lateral gill, no posterior gill, and a large terminal sucker on the median arm (Table 1).

Our specimens of *Pneumodermopsis* ***spoeli*** from Heron Island were smaller than those from Lizard Island and displayed three ciliary bands (on the head, trunk, and posterior end), which are polytrochous larval characteristics (Figure 2). These specimens are considered to be juveniles because the wings and footlobes are not fully developed. Anterior and median ciliary bands are usually lost as an animal grows. However, LALLI (1972) described neoteny in the gymnosome *Paedoclione doliiformis* Danforth, 1907, from the northwestern Atlantic, this possessing three ciliary bands even when in a reproductive state.

Species identification within the family Pneumodermatidae is greatly facilitated by detailed examinations of live animals and their extended buccal apparatus. In the absence of this, many species descriptions have been based on contracted preserved specimens, and are therefore often incomplete and confusing. Biological data on pneumodermatids is seriously lacking.

Etymology: The specific name ***spoeli*** is given in honor of Dr. S. van der Spoel of the Institute of Taxonomic Zoology, University of Amsterdam.

ACKNOWLEDGMENTS

Financial assistance was kindly provided by the Australian Biological Resource Study, the Australian Coral Reef Society, the Hawaiian Malacological Society, and the University of Queensland Research Grants Scheme. Special thanks are extended to Heron Island and Lizard Island Research Stations, to Dr. S. van der Spoel for his constructive comments and advice, and to Dr. R. Willan for his comments on an early draft of this paper.

LITERATURE CITED

GREENWOOD, J. G. & L. J. NEWMAN. 1985. Pteropod molluscs from Australian and Papua New Guinean waters. Australian Biological Resource Study Report. 32 pp.

LALLI, C. M. 1972. Food and feeding of *Paedoclione doliiformis* Danforth, a neotenous gymnosomatous pteropod. Biol. Bull. 143:392–402.

VAN DER SPOEL, S. 1973. *Pneumodermopsis teschi* n. sp., and notes on some other Pteropoda of the "Thor" Expeditions 1903–1910 (Gastropoda). Bull. Zool. Mus. Amsterdam 3(9): 53–64.

VAN DER SPOEL, S. 1976. Pseudothecosomata, Gymnosomata and Heteropoda (Gastropoda). Bohn, Scheltema, and Holkema: Utrecht. 484 pp.

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Four New *Sonorella* (Gastropoda: Pulmonata: Helminthoglyptidae) from Northwestern Sonora, Mexico

by

EDNA NARANJO-GARCIA

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, U.S.A.

Abstract. Four new species of *Sonorella,* three from the Sierra el Viejo and one from the Sierra Pico, Sonora, Mexico, are described. The Sierra Pico is currently the southwesternmost known locality for this genus. Relationships with Arizona species are discussed. *Sonorella ambigua verdensis* Pilsbry, 1939, is elevated to specific status.

INTRODUCTION

In February 1980, several land snail shells were found scattered among rocks in the Sierra el Viejo in northwestern Sonora. Dissection of one adult animal revealed that it was a new species of *Sonorella,* with a verge unlike that of any other known species.

In November 1980, live adults were taken from the limestone outcrops in the same general locality but farther northwest, ca. 2.5 km airline distance from the first location. Dissection of these specimens, however, revealed an entirely different and distinctive verge, even though the shells were not distinguishable from those collected in February. Another field party to the Sierra el Viejo in November 1981 explored a large area of the central deep canyon that runs westerly from the main north-south ridge and additional specimens of the second species were found. This party then explored another range of mountains, the Sierra Pico, just south of the Sierra el Viejo, where still another new species of *Sonorella* was found.

During October 1984, another exploration in the northern part of the range located live adults which, upon dissection, proved to be a fourth new species. The four new species are described below.

The habitat of these four new species of *Sonorella* is within the Lower Colorado River Valley subdivision of the Sonoran Desert according to the criteria of biotic communities of Turner & Brown (1982:190). This subdivision is the driest of the Sonoran Desert owing to a combination of low precipitation, high temperature, and low elevation in most of the area. The principal vegetation includes: Saguaro (*Carnegiea gigantea*), Palo Verde (*Cercidium microphyllum*), Cat Claw Acacia (*Acacia greggii*), Elephant Tree (*Bursera microphylla*), Ironwood (*Olneya tesota*), Creosote Bush (*Larrea tridentata*), Brittle Bush (*Encelia farinosa*), Senita (*Lophocereus schottii*), Organ Pipe Cactus (*Stenocereus thurberi*), Ocotillo (*Fouquieria splendens*), Teddy Bear Cholla (*Opuntia bigelovii*), Desert Lavender (*Hyptis emoryi*), Shrubby Spurge (*Euphorbia misera*), and Palo de Asta (*Cordia parvifolia*).

DESCRIPTIONS

Family Helminthoglyptidae Pilsbry, 1939

Genus *Sonorella* Pilsbry, 1900

Sonorella ***burgessi*** Naranjo-Garcia, sp. nov.

(Figures 1, 2)

Description of shell of holotype: Shell depressed, heliciform, glossy, light tan, with a narrow light brown spiral band on rounded shoulder; umbilicate, the umbilicus contained 5.8 times in the diameter of the shell, slightly covered by the reflected columellar lip. Embryonic shell of 1¼ whorls, lustrous; apex with extremely fine growth lines, and with post-apical surface roughened by closely spaced radial wrinkles. Post-embryonic whorls shiny lustrous, marked by light growth wrinkles. The last ⅛ of the body whorl descends sharply from the shoulder of the penultimate whorl. Aperture oblique, rounded, with peristome slightly expanded; margins converging; parietal callus thick;

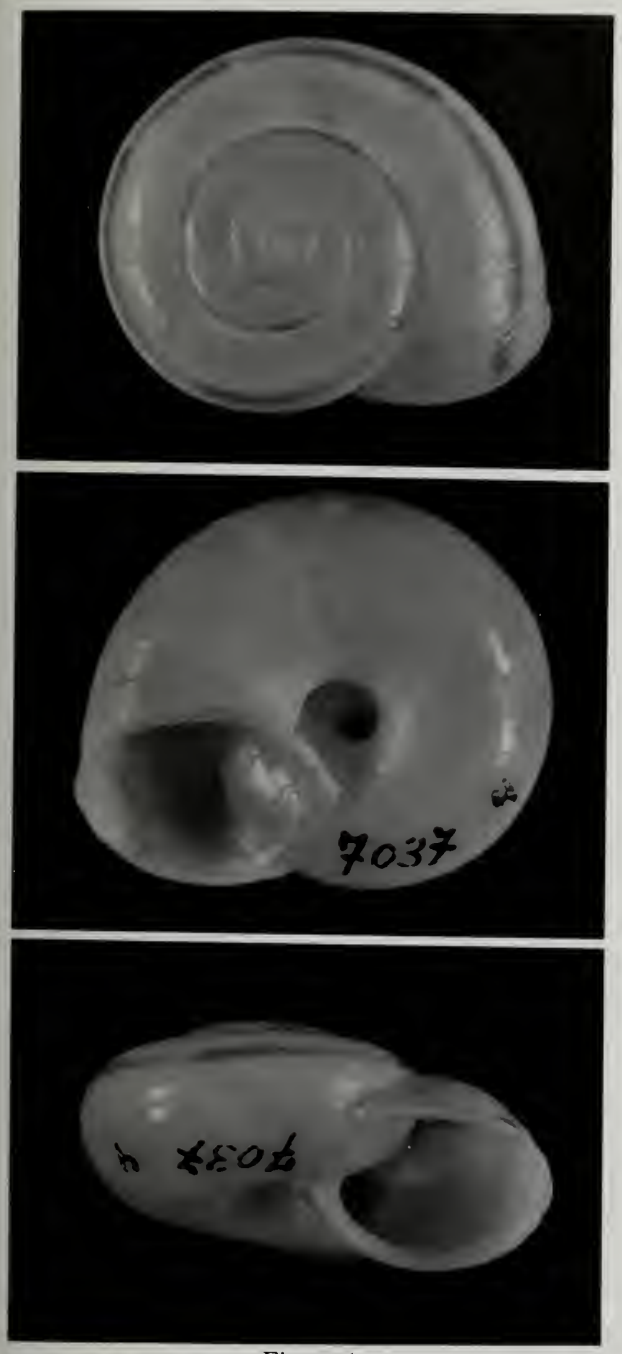

Figure 1

Sonorella ***burgessi*** Naranjo-Garcia, sp. nov. Shell of holotype, SBMNH 34933. Apical view, top; umbilicus, middle; aperture, bottom.

inner lip partly covering umbilicus. Shell measurements: diameter 19.6 mm, height 9.6 mm, umbilicus 3.4 mm; whorls, 4 (Figure 1).

Reproductive anatomy of holotype: Apical organs typical of the genus. Male structures exhibit diagnostic char-

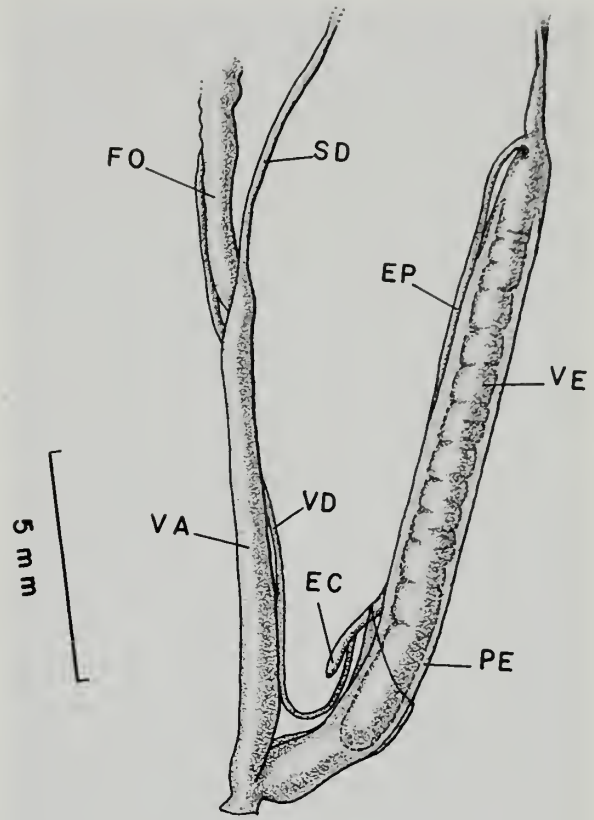

Figure 2

Sonorella ***burgessi***. Lower reproductive anatomy of holotype, SBMNH 34933. EC, epiphallic caecum; EP, epiphallus; FO, free oviduct; PE, penis; SD, spermathecal duct; VA, vagina; VD, vas deferens; VE, verge.

acters as follows: penis long, containing a long, stout, cylindrical verge; verge moderately corrugated, accordion-like, with a parabolic tip, not at all expanded; seminal duct opening terminally; penial sheath enveloping the proximal 4.3 mm of the penis; a distinct, minuscule epiphallic caecum lying free from the vas deferens. Vagina a slender cylinder, scarcely wider at base than at apical region (close to free oviduct). Measurements as follows: penis 15.9 mm, verge 12.4 mm, epiphallic caecum 1.0 mm, vagina 10.0 mm (Figure 2).

Type locality: Sierra el Viejo, Sonora, Mexico, at base of NE-facing limestone cliffs, on ridge SW of canyon junction where road from W turns N; elevation ca. 2100 ft (640 m); 30°19′N, 112°20′W; ca. 7 km E of El Plomito. Collector: T. L. Burgess, 20 February 1980.

Variations in paratypes: Ten paratypes were obtained, all of them only shells, the smallest measuring 17.5 mm in diameter and the largest measuring 20.4 mm. All exhibited the sculpture characteristic of the holotype.

Disposition of types: Holotype: Santa Barbara Museum of Natural History No. SBMNH 34933. Paratypes: Wal-

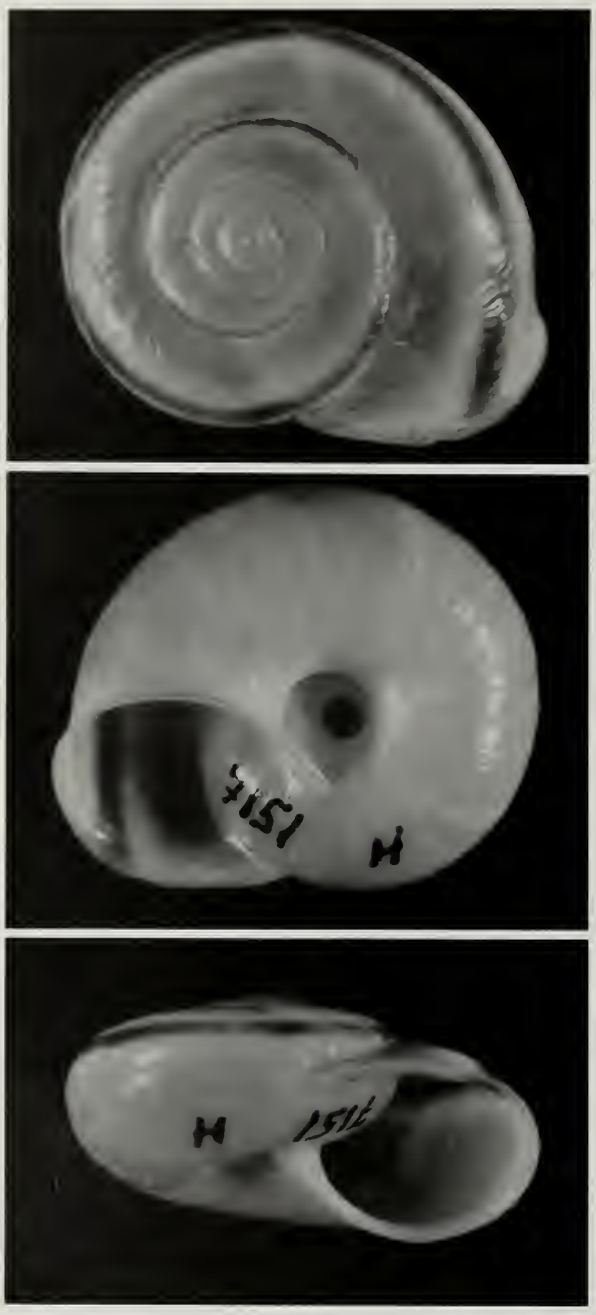

Figure 3

Sonorella ***pratti*** Naranjo-Garcia, sp. nov. Shell of holotype, SBMNH 34936. Apical view, top; umbilicus, middle; aperture, bottom.

ter B. Miller collection No. 7037, E. Naranjo-Garcia collection No. 378.

Etymology: This species is named after T. L. Burgess, the biologist who found the first specimen and brought it back for identification.

Sonorella ***pratti*** Naranjo-Garcia, sp. nov.

(Figures 3, 4)

Description of shell of holotype: Shell depressed, heliciform, light brown, with chestnut spiral band on well rounded shoulder; umbilicate, umbilicus contained 4.8 times in diameter of shell. Aperture barely covered by the reflected columellar lip. Embryonic shell of 1¼ whorls marked by microscopic, hyphen-shaped papillae, arranged in parallel spirals on top of the closely spaced radial wrinkles at the outer half of the whorl; body whorl with faint, parallel, spiral grooves impressed on its upper surface; parietal callus thin. Shell measurements: diameter 19.3 mm, height 9.7 mm, umbilicus 4.0 mm; whorls, 4¼ (Figure 3).

Reproductive anatomy of holotype: Ovotestis and female structures as in other *Sonorella*. Diagnostic characters of male structures: penis long, containing a long, stout, club-shaped, cylindrical, smooth verge having an enlarged broadly conic, invaginable tip; penial sheath encasing the proximal 4 mm of the penis. Epiphallus shorter than penis; epiphallic caecum minute ca. 1.3 mm, buried in the connective tissue of the vas deferens. Vagina ca. half the length of penis, cylindric, barely tapering to the gonopore. Measurements as follows: penis 22.0 mm, verge 17.5 mm, vagina 11.5 mm (Figure 4).

Type locality: Sierra el Viejo, Sonora, Mexico, in north facing limestone rockpiles, at base of cliffs, at mouth of large, central canyon, running westerly, at point 9.5 road miles (15.2 km) north and 4.5 road miles (7.2 km) east of El Plomito; 30°20′N, 112°20.8′W; elevation ca. 1650 ft (500 m). Type lot collected by W. B. Miller, W. L. Pratt, and University of Arizona Bio. 580 students, 21–22 November 1980.

Variations in paratypes: Twenty-eight paratypes were obtained, the largest specimen measuring 21.3 mm in diameter and the smallest measuring 17.7 mm. All but two of the unworn shells exhibited the characteristic sculpture of the holotype; the two exceptions had no papillae on the embryonic shell and no spiral grooves on the body whorl. Twelve dissections were made, and all showed the typical large, stout, club-shaped verge; some had the tip in varying stages of invagination.

Disposition of types: Holotype: Santa Barbara Museum of Natural History No. SBMNH 34936. Paratypes: National Museum of Natural History, Smithsonian Institution No. USNM 859304, Academy of Natural Sciences of Philadelphia No. ANSP 367154, Field Museum of Natural History No. FMNH 205920, University of Texas at El Paso No. 10389, Universidad Nacional Autónoma de México Colección Malacológica No. 1207, Walter B. Miller collection No. 7151.

Etymology: This species is named after my colleague Dr. William L. Pratt.

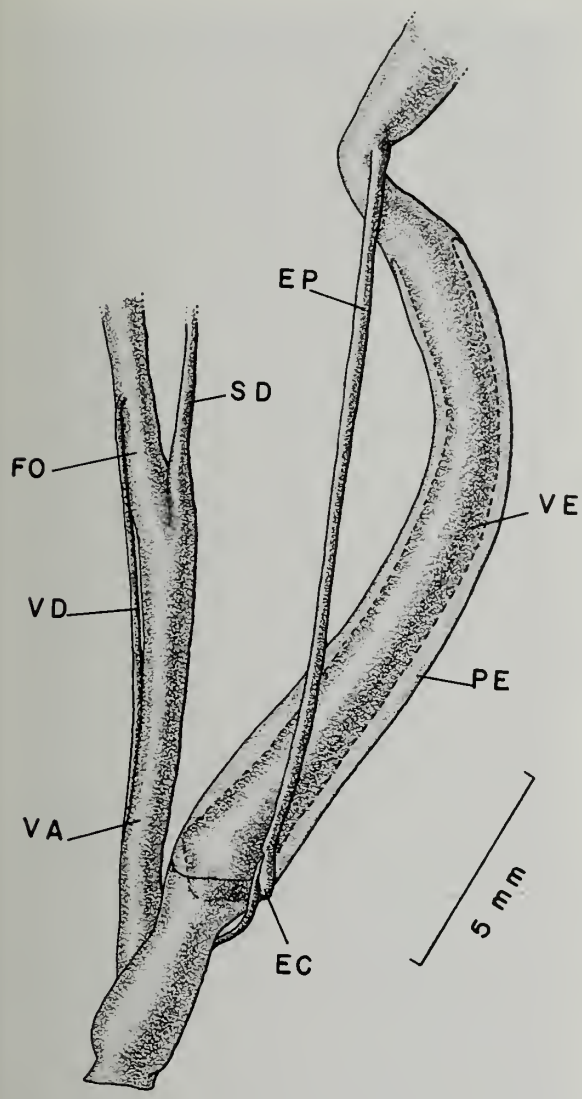

Figure 4

Sonorella ***pratti***. Lower reproductive anatomy of holotype, SBMNH 34936. EC, epiphallic caecum; EP, epiphallus; FO, free oviduct; PE, penis; SD, spermathecal duct; VA, vagina; VD, vas deferens; VE, verge.

Sonorella ***rothi*** Naranjo-Garcia, sp. nov.

(Figures 5, 6)

Description of shell of holotype: Shell depressed, globose, light tan, with a light brown spiral stripe on shoulder; shoulder round. Umbilicate, umbilicus contained 5.8 times in shell diameter. Embryonic shell of 1¼ whorls, apex with fine growth lines, thereafter the entire surface marked by numerous, closely spaced, hyphen-shaped papillae arranged in parallel, descending spirals; traces of a few scattered round papillae on subsequent whorls; shallow, parallel spiral grooves present on the last fourth of the body whorl near the suture; parietal callus very thin. Shell measurements: diameter 20.3 mm, height 11.9 mm, umbilicus 3.5 mm; whorls, 4⅓ (Figure 5).

Figure 5

Sonorella ***rothi*** Naranjo-Garcia, sp. nov. Shell of holotype, SBMNH 34934. Apical view, top; umbilicus, middle; aperture, bottom.

Reproductive anatomy of holotype: Ovotestis and female structures as in other *Sonorella*. The male structures exhibit diagnostic characters as follows: penis long, con-

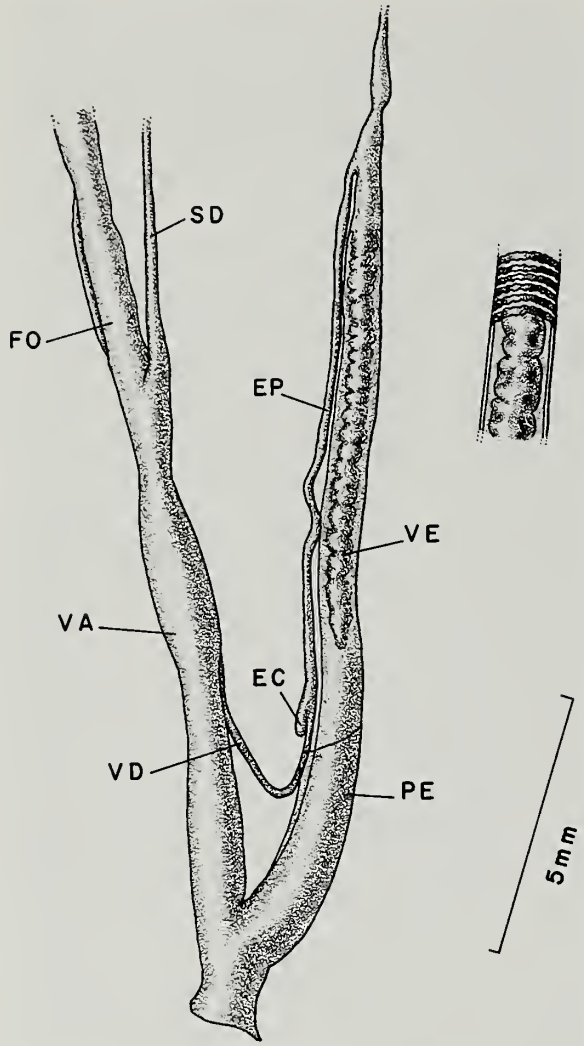

Figure 6

Sonorella ***rothi***. Lower reproductive anatomy of holotype, SBMNH 34934. EC, epiphallic caecum; EP, epiphallus; FO, free oviduct; PE, penis; SD, spermathecal duct; VA, vagina; VD, vas deferens; VE, verge.

taining a thin, corrugated and dimpled verge, with an acutely pointed tip. The upper ⅔ of inner walls of penis glandular. Penial sheath ⅓ as long as the penis; small epiphallic caecum lying free from the vas deferens. Vagina almost cylindrical, the upper region widening ovally, the middle narrowing slightly and the region close to the gonopore widening again; the inner walls are glandular (Figure 6). Measurements: penis 14.7 mm, verge 7.9 mm, penial sheath 4.6 mm, epiphallic caecum 0.7 mm, vagina 10.2 mm.

Type locality: NW end of Sierra Pico (not "Picu"; see Office of Geography, 1956:467), Sonora, Mexico, in igneous rocks at base of cliffs, along road from El Plomito to Puerto Libertad, at 14.9 road miles (23.8 km) from El Plomito; elevation ca. 1200 ft (365 m); 30°0.5′N, 112°27′W. Type material collected by W. B. Miller, B. Roth, and J. E. Hoffman, 13 November 1981.

Variations in paratypes: Five live specimens and 25 shells were collected in the type lot, the largest shell measuring 21.7 mm in diameter and the smallest measuring 18.5 mm. The unworn shells exhibited the characteristic sculpture of the holotype in various degrees. Only two of the live specimens were adult, and their dissection revealed a similar thin, corrugated, dimpled, sharply pointed verge.

Disposition of types: Holotype: Santa Barbara Museum of Natural History No. SBMNH 34934. Paratypes: National Museum of Natural History, Smithsonian Institution No. USNM 859305, Academy of Natural Sciences of Philadelphia No. ANSP 367153, Field Museum of Natural History No. FMNH 205921, University of Texas at El Paso No. UTEP 10390, Universidad Nacional Autónoma de México Colección Malacológica No. 1208, Walter B. Miller collection No. 7242, E. Naranjo-Garcia collection No. 374.

Etymology: This species is named after my friend and colleague Dr. Barry Roth.

Sonorella ***seri*** Naranjo-Garcia, sp. nov.

(Figures 7, 8)

Description of shell of holotype: Shell depressed, heliciform, light brown with a narrow chestnut band on the shoulder. Umbilicate, umbilicus contained 4.7 times in shell diameter. Embryonic shell of 1¼ whorls, apex smooth; first half of post-apical embryonic whorls with well defined growth wrinkles gradually covered by punctate papilla; the second half with hyphen-like papillae producing a reticulate effect; reticulation disappearing gradually on later whorls, leaving only growth wrinkles and a shiny periostracum; parietal callus thin. Shell measurements: diameter 18.9 mm, height 8.9 mm, umbilicus 4.0 mm; whorls, 4 (Figure 7).

Reproductive anatomy of holotype: Ovotestis and female structures as in other *Sonorella*. Penis long, containing a long, smooth verge slightly wider near the end, terminating in attenuated tip. Penial sheath short, less than ⅕ the length of the penis. Epiphallis shorter than penis, epiphallic caecum minute, ca. 1.0 mm. Vagina tubular, slightly tapering to the gonopore; inner walls glandular, length ca. ½ as long as the penis. Measurements as follows: penis 23.7 mm, verge 21.1 mm, penial sheath 5.0 mm, vagina 12.6 mm (Figure 8).

Type locality: Sierra el Viejo, Sonora, Mexico, in N-facing limestone piles at north end of range, 30°24.1′N, 112°22.5′W, elevation ca. 1800 ft (550 m). Type specimens collected by W. B. Miller, J. E. Hoffman, G. Fink, and E. Naranjo-Garcia, 20 October 1984.

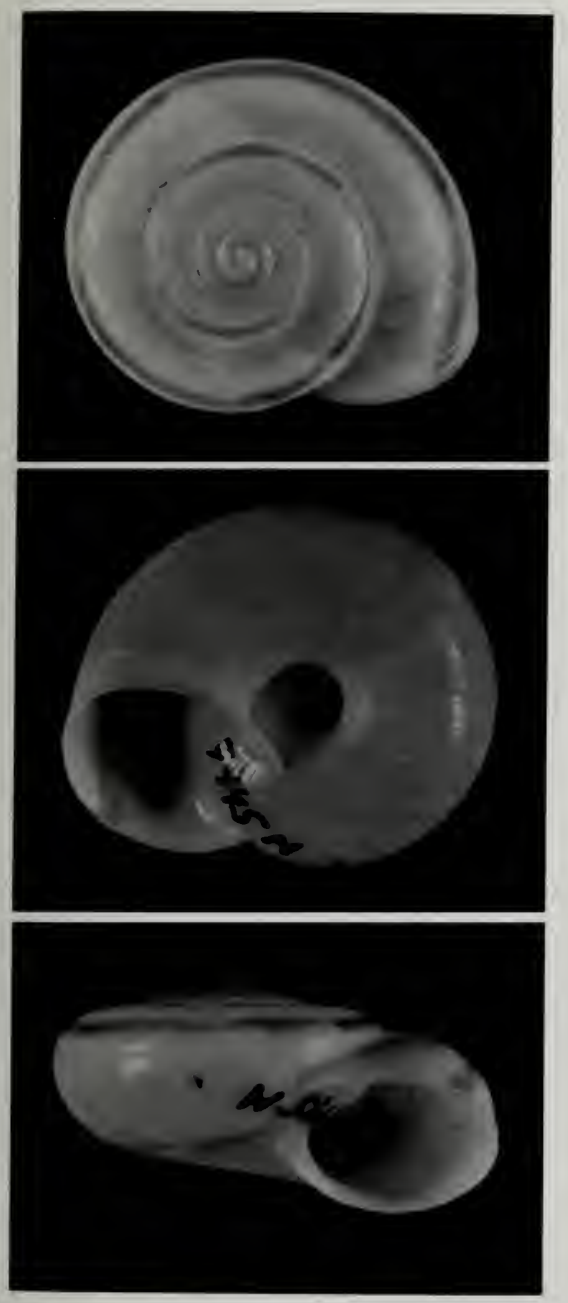

Figure 7

Sonorella seri Naranjo-Garcia, sp. nov. Shell of holotype, SBMNH 34935. Apical view, top; umbilicus, middle; aperture, bottom.

Variations in paratypes: Thirty-five paratypes were obtained, including some live ones, the smallest measuring 16.0 mm in diameter and the largest measuring 19.6 mm. The fresh, unworn shells exhibited a sculpture similar to that of the holotype.

Disposition of types: Holotype: Santa Barbara Museum of Natural History No. SBMNH 34935. Paratypes: National Museum of Natural History, Smithsonian Institution No. USNM 859306, Academy of Natural Sciences of Philadelphia No. ANSP 367155, Field Museum of Natural History No. FMNH 205922, University of Texas at El Paso No. UTEP 10391, Universidad Nacional Autónoma de México Colección Malacológica No. 1209, E. Naranjo-Garcia collection No. 405, Walter B. Miller collection No. 7445.

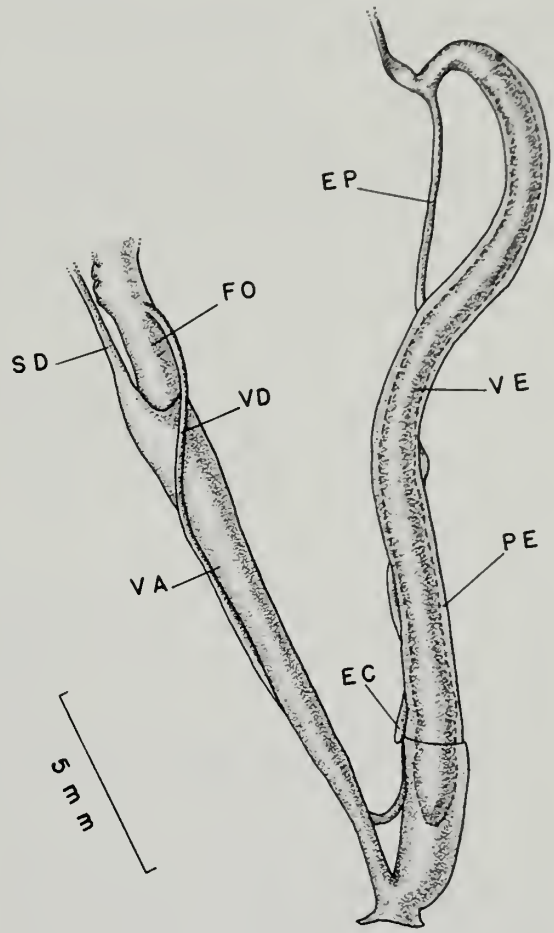

Figure 8

Sonorella seri. Lower reproductive anatomy of holotype, SBMNH 34935. (Composite drawing based on holotype and one other specimen, because in the holotype the female side is folded.) EC, epiphallic caecum; EP, epiphallus; FO, free oviduct; PE, penis; SD, spermathecal duct; VA, vagina; VD, vas deferens; VE, verge.

Etymology: This species is named for the natives living in the vicinity of the type locality, the Seri People.

DISCUSSION

The shells of *Sonorella* ***burgessi***, *S.* ***pratti***, *S.* ***rothi***, and *S.* ***seri*** are essentially similar in appearance and, although there are distinguishable differences in the sculpture of fresh, unworn shells, the range of variation in the number of embryonic papillae and in the degree of faintness or prominence of body-whorl spiral grooves renders these

diagnostic characters unreliable. The size and shape of the verge, however, provide an immediate, unequivocal diagnosis.

Sonorella ***burgessi*** is probably most closely related to *Sonorella ambigua* Pilsbry & Ferriss, 1915, and *Sonorella* ***verdensis*** Pilsbry, 1939, here elevated to specific status. In 1967 MILLER ranked *S.* ***verdensis*** as a subspecies of *S. ambigua* because the verge of these two species looked very much alike. However, the verge of *S.* ***verdensis*** is more than one-third longer than that of *S. ambigua*. Furthermore these two taxa are geographically separated by over 160 km, without intervening populations. Accordingly, they are considered to be reproductively isolated.

The male reproductive anatomy of *Sonorella* ***burgessi*** shows an almost cylindrical verge, smooth, with some foldings, and a well rounded tip, while *S. ambigua* has a club-shaped verge, corrugated the last third of its length, with the thickest part behind the broad tip. In *S.* ***verdensis*** the shape of the reproductive structures is about the same as that of *S. ambigua*; however, the dimensions are ca. one-third larger. The length of the structures is the shortest in *S.* ***burgessi***. The vagina is almost cylindrical, tapering slightly to its apical end; in *S. ambigua* and *S.* ***verdensis*** the vagina is cylindrical.

The reproductive anatomy of *Sonorella* ***pratti*** resembles that of *Sonorella imitator* Gregg & Miller, 1972. The differences between them are: the shell of *S. imitator* is heavier and darker in color, and it has a taller spire; as a consequence the shell is more globose-helicoid than in *S.* ***pratti,*** which is flatter. The apical sculpture possesses round papillae on top of the strong growth wrinkles; subsequent whorls bear fine stippling except on the body whorl. The shell of *S.* ***pratti*** is light, and light tan in color, and the shape is depressed-helicoid. The growth wrinkles are fine as are the spiral descending threads; subsequent whorls are smooth. In the reproductive system the main differences are in the vagina of *S. imitator* which is about the same size as the verge (one-eighth shorter), while in *S.* ***pratti*** it is one-half the length of the verge. The free oviduct and the penis in *S. imitator* are shorter than in *S.* ***pratti***.

Sonorella ***rothi*** has a verge somewhat similar in shape to those of *Sonorella ashmuni* Bartsch, 1904, and *Sonorella sabinoensis sabinoensis* Pilsbry & Ferriss, 1919, but with significant differences in proportions. In *S. s. sabinoensis* the length of the verge is more than two-thirds the length of the penis whereas in *S.* ***rothi*** and *S. ashmuni* it is only about one-half the length of the penis. There are also significant differences in the proportional sizes and shapes of the vagina. In *S. s. sabinoensis* and *S. ashmuni*, it is cylindrical and as long as the penis; in *S.* ***rothi,*** it forms an oval node at its apical end and it is less than two-thirds the length of the penis.

Sonorella ***seri*** seems to be most closely related to *Sonorella parva* Pilsbry, 1905, and *Sonorella virilis virilis* Pilsbry, 1905. The shape of the verge is similar in these three species. The length of the penis of *S.* ***seri*** is about equal to that of *S. parva,* but shorter than that of *S. v. virilis*; the vagina equals the length of the penis in *S. parva,* while in *S.* ***seri*** it is about one-half, and in *S. v. virilis* it is about two-thirds the length of the penis. The shape of the vagina is different in all three species. In *S.* ***seri*** it is a narrow cylinder that tapers to the basal end, in *S. parva* a cylinder with a swollen node near the middle, and in *S. v. virilis* a long cylindrical tube without node or tapering end.

From these explorations in northwestern Sonora it can now be stated that the southwesternmost limit of the genus *Sonorella* lies in the Sierra Pico, although it is possible that it might extend a few kilometers to the west where similar physical and biotic conditions exist but no explorations have yet been made. Beyond the Sierra de Aguirre the situation changes abruptly and a different habitat reveals populations of *Eremarionta rowelli mexicana* (Pilsbry & Lowe, 1934). No species of *Eremarionta* has ever been found sympatrically with species of *Sonorella* (BEQUAERT & MILLER, 1973).

ACKNOWLEDGMENTS

I wish to thank Walter B. Miller, who collected and dissected many of the specimens and provided me with the material from his early trips to the Sierra el Viejo area and Arizona. I am grateful to W. B. Miller and Jim Hoffman for their companionship in the field. R. Sidner helped revise the manuscript. Consejo Nacional de Ciencia y Tecnologia provided grant support for my studies.

LITERATURE CITED

BEQUAERT, J. C. & W. B. MILLER. 1973. The mollusks of the arid southwest with an Arizona check list. University of Arizona Press: Tucson, Arizona. 271 pp.

MILLER, W. B. 1967. Anatomical revision of the genus *Sonorella* (Pulmonata: Helminthoglyptidae). Ph.D. Dissertation, University of Arizona. 293 pp., illus., maps.

OFFICE OF GEOGRAPHY (Dept. of Interior). 1956. Mexico: official standard names. Washington, D.C. 750 pp.

TURNER, R. M. & D. E. BROWN. 1982. Sonoran desertscrub. *In:* D. E. Brown (ed.), Biotic communities of the American southwest—United States and Mexico. Desert plants (special issue). Vol. 4(1-4):190-200.

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A New *Helminthoglypta* (*Rothelix*) (Gastropoda: Pulmonata: Helminthoglyptidae) from Warner Springs, San Diego County, California

by

RICHARD L. REEDER

Faculty of Biological Science, University of Tulsa, Tulsa, Oklahoma 74104, U.S.A.

AND

WALTER B. MILLER

Department of Ecology and Evolutionary Biology, The University of Arizona, Tucson, Arizona 85721, U.S.A.

Abstract. A new species of land snail, *Helminthoglypta* (*Rothelix*) ***warnerfontis,*** is described and its relationships within the subgenus *Rothelix* are described.

INTRODUCTION

This paper on a new *Helminthoglypta* is part of our continuing investigations of members of this genus in San Diego County and elsewhere in southern California (MILLER, 1985; REEDER, 1986; REEDER & MILLER, 1986a, b, 1987). We have relied heavily on material collected by the late Wendell O. Gregg as well as several personal collections in the Warner Springs area over the last 27 years.

Helminthoglypta (*Rothelix*) ***warnerfontis***
Reeder & Miller, sp. nov.

(Figures 1–4)

Diagnosis: A medium-sized, sub-globose *Helminthoglypta* (*Rothelix*) with a densely papillose shell and an open umbilicus; with penial sheath enveloping only the anterior chamber of lower part of penis and combined length of vagina and oviduct nearly equal to that of the lower part of the penis.

Description of shell of holotype: Shell (Figures 2–4) of moderate size, depressed, with conic spire, umbilicate, the umbilicus contained about 9.5 times in the diameter of the shell. Color tan to brown with a thin reddish-brown band on the rounded shoulder. Aperture ovate–lunate with peristome thickened, reflected moderately, and expanded only slightly at its columellar junction. Embryonic shell of 1¾ whorls, finely granulose. Postembryonic whorls with radial growth wrinkles and densely papillose with minute, evenly spaced papillae extending on to the base of the shell and into the umbilicus. Penultimate and body whorls with spirally arranged incised lines which are present both above and, more weakly, below the shoulder of the body whorl. Diameter 19.0 mm, height 11.4 mm, umbilicus 2.5 mm, number of whorls 6¼.

Reproductive anatomy of holotype: The genitalia (Figure 1) are typical of the subgenus, with a long, spacious atrial sac having a small dart sac at its proximal end and having two mucous glands with mucous bulbs, the ducts of which unite before entering the proximal end of the atrial sac. The vagina opens into the atrial sac at the proximal end. The spermatheca is spherical with a long duct having a spermathecal diverticulum diverging at a point approximately one-third of the way along the duct above its junction with the vagina. The penis has upper and lower divisions, the upper part of the penis being a shorter, narrow, double-walled tube. The lower part is single-tubed with a long, sausage-shaped anterior chamber and a shorter posterior chamber, the latter set off sharply from the anterior region by a venturi-like constriction and tapering sharply to its junction with the upper penis. A prominent connective tissue band unites the vas deferens

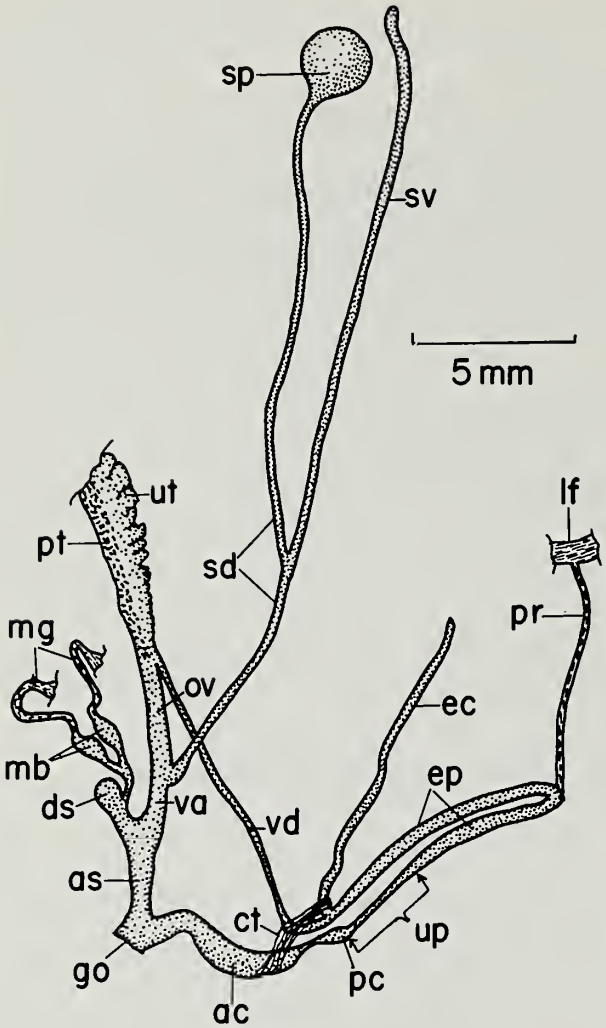

Figure 1

Anterior portion of reproductive system of holotype of *Helminthoglypta* (*Rothelix*) ***warnerfontis*** Reeder & Miller, sp. nov. Drawing prepared from projection of stained whole mount, WBM 6032, collected 23 Nov. 1972 at the type locality; arrows indicate limits of double-tubed upper part of the penis. ac, anterior chamber of lower part of penis; as, atrial sac; ct, connective tissue binding penis to vas deferens; ds, dart sac; ec, epiphallic caecum; ep, epiphallus; go, genital orifice; lf, portion of lung floor to which penial retractor attaches; mb, mucus bulbs; mg, initial portion of mucus gland membranes; ov, oviduct; pc, posterior chamber of lower part of penis; pr, penial retractor muscle; pt, prostate; sd, spermathecal duct; sp, spermatheca; sv, spermathecal diverticulum; up, upper part of penis; ut, uterus; va, vagina; vd, vas deferens.

with the upper portion of the anterior chamber of the lower penis. The epiphallus is of moderate length with a short epiphallic caecum. The penial retractor muscle attaches to the epiphallus. Measurements of anatomical structures are as follows:

Penis	9.64 mm
Epiphallus	12.9 mm
Epiphallic caecum	10.4 mm
Spermathecal duct	22.4 mm
Spermathecal diverticulum	17.5 mm
Vagina and oviduct combined	5.3 mm

Variations in paratypes: A total of 34 adult shells and 35 immatures was examined. Of 32 measurable adults the largest was 19.5 mm in diameter and 10.5 mm in height and the smallest measured 14.9 mm in diameter and 9.5 mm in height. All of the shells exhibited the radial growth lines and the characteristic densely papillose condition. Twelve adults and 15 immatures exhibited the spirally arranged incised lines.

Disposition of types: Holotype: Santa Barbara Museum of Natural History no. 34943. Paratypes: The Academy of Natural Sciences of Philadelphia no. 368246; U.S. National Museum no. 860400; W. B. Miller collection nos. 3794, 4307, and 6032; R. L. Reeder collection no. 716.

Type locality: San Diego County, California: in wood rat nests in Cañada Agua Caliente along south side of California State Highway 79, adjacent to golf course, about 1.6 km west of post office and fire station buildings in Warner Springs; 33°17.1′N, 116°39.2′W; elev. ca. 900 m (2950 ft); collected 31 Jan. 1960 (W. B. Miller and W. O. Gregg), 20 May 1962 (W. B. Miller and W. O. Gregg), 23 Nov. 1972 (W. B. Miller and R. L. Reeder) and 4 March 1985 (W. B. Miller, R. L. Reeder, and H. L. Fairbanks).

Discussion: There are now four known species of *Helminthoglypta* in the subgenus *Rothelix* Miller, 1985: *H.* (*R.*) *lowei* (Bartsch, 1918) (type species), *H.* (*R.*) *cuyamacensis* (Bartsch, 1916), *H.* (*R.*) *rhodophila* Reeder & Miller, 1987, and *H.* (*R.*) ***warnerfontis*** described above. All possess the characteristic penial features of *Rothelix,* namely a short and thin, double-tubed, upper part of the penis and a long and large lower part of the penis composed of a small posterior chamber connected to a capacious, sausage-shaped, anterior chamber by a very narrow venturi-shaped constriction. Additionally, the lower part of the penis is surrounded by a tough connective tissue which acts as a virtual penial sheath and binds it by numerous tissue threads to the vas deferens at its junction with the epiphallus. In *H. cuyamacensis* and *H. rhodophila,* this penial sheath completely envelops all of the posterior and anterior chambers whereas in *H. lowei* and *H.* ***warnerfontis*** it envelops only a part of the anterior chamber, leaving the posterior chamber and the venturi connection completely free. This characteristic is consistent in all adult specimens dissected (4 *H. cuyamacensis,* 5 *H. lowei,* 12 *H. rhodophila,* and 11 *H.* ***warnerfontis***). Accordingly, it provides a reliable diagnostic feature. Anatomically, therefore, *H.* ***warnerfontis*** appears to be most closely related to *H. lowei,* sharing similar penial characters. It differs from *H. lowei,* however, in that the female structures are proportionally larger. In *H. lowei,* the combined lengths of the vagina and oviduct are strikingly small, only about one-

Explanation of Figures 2 to 4

Helminthoglypta ***warnerfontis*** Reeder & Miller, sp. nov. Shell of holotype, SBMNH 34943; diameter 19.0 mm. Figure 2. Aperture view. Figure 3. Apical view. Figure 4. Umbilical view.

half the length of the lower part of the penis while in *H.* ***warnerfontis*** they are as long as the lower part of the penis. *Helminthoglypta* ***warnerfontis*** also differs from *H. lowei* in that it is a much smaller snail. The shell diameter of *H. lowei* ranged from 26.7 mm to 23.8 mm in 13 adult shells examined, with a mean of 24.3 mm, well above the largest specimen of *H.* ***warnerfontis,*** which is 19.5 mm in diameter.

Distribution and habitat: In 1957 and 1972, *Helminthoglypta* ***warnerfontis*** was found widely and abundantly scattered in numerous wood rat nests along Cañada Agua Caliente below Warner Springs. Shortly thereafter, however, with the advent of golf courses and human population pressure, the area was "cleaned up" and rat nests became hard to find; with their disappearance the snails also became scarce. In March 1985, we revisited the area and after considerable searching, we came up with only one dead subadult shell and one live immature. It is apparent that this population is nearing extinction. Fortunately, we found another population, albeit in a small restricted area, along the ravine just below Lost Valley Spring (33°20.7′N, 116°38.1′W), approximately 8 km (5 miles) due north of Cañada Agua Caliente, in logs and leaf mold of *Quercus agrifolia.* Snails from this population are indistinguishable from specimens from Cañada Agua Caliente; they are considered to be conspecific. Since Lost Valley Spring is in the Cleveland National Forest, it is hoped that this species may continue to survive in relative protection.

Etymology: This species was known for many years to S. S. Berry and W. O. Gregg as "the Warner Spring snail." Gregg deferred to Berry, who always intended to describe it, but ultimately ran out of time. We are pleased to con-

tinue the use of their name, substituting the Latin *fontis* (genitive of *fons*) for spring.

ACKNOWLEDGMENTS

We wish again to express our gratitude to our late colleague Wendell O. Gregg for materials used in our studies. We wish also to thank our colleagues Susan McKee for preparation of photographs of the holotype, and Lee Fairbanks for help and companionship in the field. We are also indebted to Barbara Barnard and Jan Bingham for clerical and other assistance. We also extend our gratitude to the University of Tulsa and in particular to Dr. Allen Soltow for providing funds for fieldwork.

LITERATURE CITED

Miller, W. B. 1985. A new subgenus of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae). Veliger 28(1):94–98.

Reeder, R. L. 1986. A new species of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae) from the Cuyamaca Mountains of southern California. Veliger 28(4):444–447.

Reeder, R. L. & W. B. Miller. 1986a. A new species of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae) from San Diego County, California. Proc. Biol. Soc. Wash. 99(1):137–139.

Reeder, R. L. & W. B. Miller. 1986b. A description of a new *Helminthoglypta* s.s. (Gastropoda: Pulmonata: Helminthoglyptidae) from San Diego County, California. Veliger 29(1):129–131.

Reeder, R. L. & W. B. Miller. 1987. A new *Helminthoglypta* (*Rothelix*) (Gastropoda: Pulmonata: Helminthoglyptidae) from southern California with comments on its probable evolutionary relationships. Southwestern Naturalist 32(2): 261–265.

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Studies on Distribution, Degree of Aerial Exposure, and Competitive Interactions in Four Species of Tropical Intertidal Gastropods

by

MAY W. YIPP[1] AND THOMAS H. CAREFOOT

Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada V6T 2A9

Abstract. The vertical distributions of the limpet *Acmaea jamaicensis* and the littorines *Nodilittorina tuberculata, N. ziczac,* and *Littorina meleagris* were investigated on a vertical limestone block on the west coast of Barbados, W.I. Three vertical experimental plots and one vertical control plot were fenced off on the limestone block. In each of the experimental plots all gastropods except for one species of littorinid under study were removed. The control plot contained the natural density of all species of gastropods. Significant differences in distributional patterns were recorded between the experimental and control plots for all littorinid species after a 20-day period. When *L. meleagris* was living sympatrically with different experimental densities of *A. jamaicensis,* its distributional patterns were also shown to differ significantly, while reciprocal effects of *L. meleagris* on *A. jamaicensis* were not noted. Both sets of experimental data indicated the existence of interspecific competition among the four species of gastropods. In addition, variation among the three littorinids in functional morphology of the mantle cavity, and survival in air and water, were investigated, and the significance of these findings to the vertical distributional patterns of the four species was discussed.

INTRODUCTION

Species of littorinid snails are common inhabitants of upper intertidal and supratidal areas on many ocean shores. In this high intertidal-level position, conditions may be more terrestrial than marine, and the animals may spend considerable portions of their lives exposed to air, or perhaps wetted only from wave splash or spray. As a consequence, drying, exposure to damaging wavelengths of light, reduced feeding time, and possible heightened risk of predation may be important determinants of survival and distribution.

The means by which motile organisms position themselves at specific levels on the shore have commanded much attention over the past two decades, and gastropods have featured in a number of important studies of this topic (*e.g.,* CONNELL, 1961, 1970; DAYTON, 1971; MENGE, 1976; LUBCHENKO & MENGE, 1978; GARRITY, 1984). Competition, as one specific mechanism involved in modifying and regulating community patterns in the intertidal area, has been extensively investigated in gastropods (KOHN, 1959; HAVEN, 1973; STIMSON, 1973; BRANCH, 1975a, b, 1976; UNDERWOOD, 1976, 1978; BLACK, 1979; CREESE, 1982; CREESE & UNDERWOOD, 1982). However, while competitive interactions can be identified in gastropods and their effects often measured (by removing the competitive dominant), the actual function of competition in regulating patterns of distribution in intertidal snail populations is not clear. This has been emphasized by UNDERWOOD (1979) in his comprehensive review of the ecology of intertidal gastropods and, more recently, by CREESE (1982) and CREESE & UNDERWOOD (1982), who have shown that a competitively dominant species of grazing snail, while reducing the numbers or growth rates of other species of grazing snails, may not affect their patterns of distribution. Notwithstanding the observation by CHOAT (1977), that removal of the limpet *Collisella* (now *Lottia*) *digitalis* from its high-level intertidal position allowed another limpet *C. paradigitalis* (now *Lottia strigatella*; LINDBERG, 1986) to move to a higher than normal position, CREESE & UNDERWOOD (1982) suggest that no competitive interaction between any species of intertidal grazing gastropods has been demonstrated to determine limits of distribution,

[1] Present address: Department of Applied Science, Hong Kong Polytechnic, Hong Kong.

save for the special case of territorial limpets (*e.g.*, as in the studies of SUTHERLAND [1970], STIMSON [1973], and BLACK [1979]).

In the present study we have investigated the possible role of competitive exclusion in defining distribution of three species of littorinid snails in Barbados, West Indies: *Nodilittorina tuberculata* Menke, 1928, *Nodilittorina* (*Nodilittorina*) *ziczac* (Gmelin, 1791), and *Littorina meleagris* Potiez & Michaud, 1838. *Nodilittorina tuberculata* is the numerically dominant of the three species, with a vertical distribution almost identical to that of *N. ziczac*. *Littorina meleagris* occurs at the lowest tidal level and is spatially separated from the other two littorinids, but its distribution overlaps almost completely that of the limpet *Acmaea jamaicensis* Gmelin, 1791. The biology of this limpet species is not well known. It appears to be a non-homing form, but with fairly strong "site-attachment" tendencies (*i.e.*, its movements are limited). Because of its potential interaction with *L. meleagris*, it was included in certain of the studies on competition. In addition, we investigated the degree of aerial exposure, survival in air and water, and aspects of ctenidial morphology in relation to possibly differing modes of oxygen uptake in the three littorinid species.

Description of Habitat

The study site was located on the west coast of Barbados, West Indies, at Six Men's Bay (13°16′N, 59°38′W), 6.5 km north of the Bellairs Research Institute of McGill University. It consisted of an irregular beach-rock platform which was exposed at low tides and was occupied by a variety of snails, limpets, sea urchins, and algae. Two artificial berms, constructed of symmetrical limestone blocks, faced onto the beach-rock platform. Each provided a vertical intertidal surface measuring 2.1 m wide and 1.8 m high. The bases of the blocks were about 0.45 m above mean lower low water (MLLW). The faces of the blocks were completely exposed at most low tides, and were immersed to 1.2 m height and splashed to 2.0 m height on high monthly spring tides. Predominant gastropods on the vertical faces were the littorines *Nodilittorina tuberculata* (1.7 cm in length), *N. ziczac* (1.5 cm), and *Littorina meleagris* (0.5 cm), and the limpet *Acmaea jamaicensis* (1.3 cm). A variety of green algae and mixed diatoms formed a film over the vertical faces of the limestone blocks. Mean daily air temperature during the period of study (May–June) was 28–30°C; surface sea temperature was 28.5°C; and surface sea salinity was 32.0–33.0‰.

One limestone block provided the means to assess temporal changes in the distribution of each species of littorine with and without the presence of the other species of littorines. The other limestone block permitted study of the interactions between the low intertidal-inhabitants, the limpet *Acmaea jamaicensis* and the lowest-dwelling littorine *Littorina meleagris*. Preliminary observations showed that there was considerable overlap in the vertical distributions of the highest-dwelling species *Nodilittorina tuberculata* and *N. ziczac*, and some overlap of the lowest portion of the distribution of these species with that of the lowest-dwelling littorinid species *L. meleagris*, hence, providing potential for competition. Analysis of gut contents of all three species collected at high tide showed that similar foods were being eaten (see below) and the three species of littorines were also similar in their preferential occupation of depressions in the surface of the limestone; thus, competition could have been for either or both food and space.

Food Eaten

Six samples of epilithic algae were scraped from the experimental blocks using a stiff brush and fixed in 8% seawater-formalin. The samples were collected from six evenly spaced intertidal heights. Examination of the samples revealed that from 0–90 cm height in the blocks there was abundant growth of diatoms, algal sporelings, and other unicellular and filamentous species of green algae (0.45–1.35 m above MLLW), with a thicker-walled unicellular alga growing above 90 cm. Ten snails of each species were collected at high tide from the study site and preserved in 8% seawater-formalin in the field. Their stomach contents were compared to the algal samples and revealed that each species was grazing on the algal species occurring at its preferred vertical height. *Acmaea jamaicensis* and *Littorina meleagris* appeared to graze indiscriminately on algal flora occurring between 0–90 cm, and seemed to eat similar food items. *Nodilittorina tuberculata*, on the other hand, had a predominance of thick-walled unicellular algae representative of a higher intertidal position. *Nodilittorina ziczac*, though significantly overlapping the distribution of *N. tuberculata*, had more variable stomach contents indicating less selective grazing.

Competitive Interactions of Littorines

One limestone block was divided into four vertical plots, each being 50 cm in width and extending the entire intertidal height to about 20 cm above the high tide mark. Fences, constructed of 10-cm high aluminum mesh embedded in Z-SPAR epoxy putty, separated the plots and prevented animals from crossing from one to another. All snails, including limpets, were removed from three of the plots to leave one species only of littorinid snail in each of the plots; the fourth plot was left as a control. One day following this removal and thereafter at approximately 7-day intervals for 20 days, counts were made of individuals of all three littorinid species in 30-cm contiguous bands beginning from the lowest part of each plot (0 cm height in the block) and working upwards. Counts were made at both low tide and high tide (latter only from day 8–9) for each species. Temporal differences in distribution of a species in an experimental plot relative to its distribution in the control plot were analyzed using a Mann-Whitney U test. We hypothesized that if competitive in-

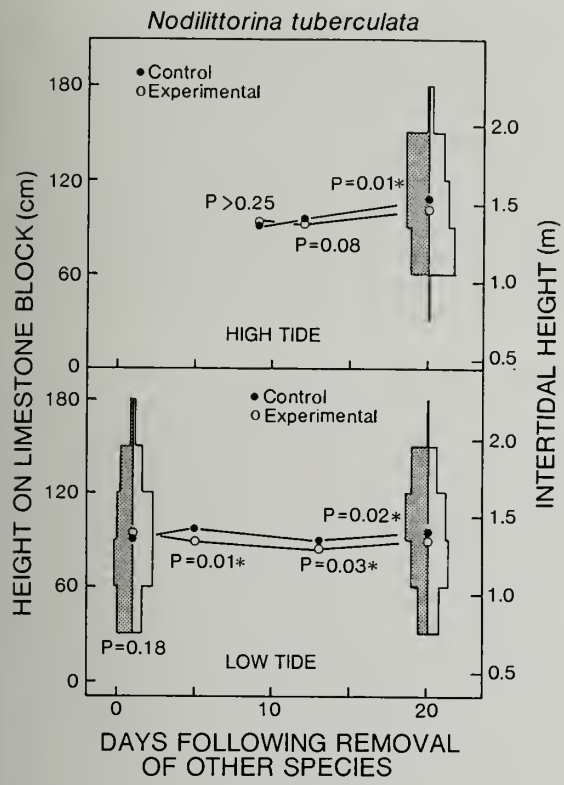

Figure 1

Temporal changes in distributional patterns of *Nodilittorina tuberculata* at high and low tides on limestone blocks in Barbados, W.I. The experimental animals occupied a plot where all other species of snails were removed. Their distribution is compared with the distribution of the same species in a control plot where all species were present. Each point represents the mean of 147–194 animals for the high-tide curves and 125–214 animals for the low-tide curves. Probability levels (one-tailed format) are determined from the Mann-Whitney U statistic calculated from the total distribution represented by each mean value. The histograms show distributions in bands of 30-cm height for each plot, expressed as percentages, for the starting and finishing days (control = closed circles, experimental = open circles). Width of each histogram indicates relative abundance.

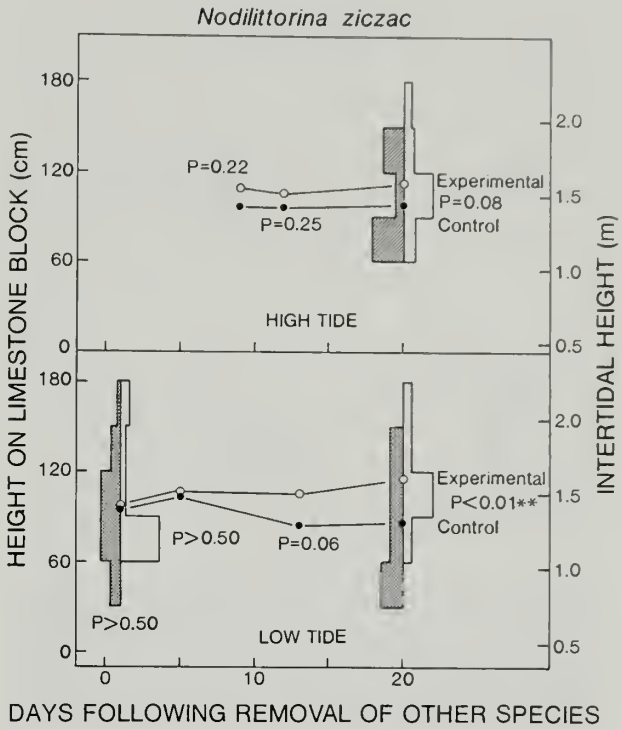

Figure 2

Temporal changes in distributional patterns of *Littorina ziczac* at high and low tides on limestone blocks in Barbados, W.I. Each point represents the mean of 20–32 animals for the high-tide curves and 19–35 animals for the low-tide curves. Probability levels (two-tailed format) are determined from the Mann-Whitney U statistic calculated from the total distribution represented by each mean value. Other details as specified for Figure 1.

teractions, possibly of the interference type, were restricting movements of the littorinid species, it would likely be downward for the uppermost species *Nodilittorina tuberculata,* upward for the lowermost species *Littorina meleagris,* and perhaps either way for the smaller of the uppermost species *N. ziczac.* Consequently, the analyses were one-tailed in the first two instances and two-tailed in the third. Because the distribution of a species in its experimental plot was compared simultaneously with its distribution in the control plot, any variation in distributional pattern due to environmental factors such as temperature, tidal exposure, or desiccation, assumed to affect a species alone or when in sympatry, would be taken into account.

Changes in distribution of each of the littorinid species in control and experimental plots over the 20-day experimental period are shown at both high and low tides in Figures 1–3. Two major points are evident from these data. First, in the absence of the other gastropod species, the distribution of a given littorinid species changed significantly (all save for *Nodilittorina ziczac* at high tide). For two of the species the direction of movement was as predicted—namely, a movement of *N. tuberculata* downwards ($P = 0.01$ and 0.02 for comparisons of control and experimental distributions in each of high- and low-tide situations, respectively; Mann-Whitney U test), and a movement of *Littorina meleagris* upwards ($P < 0.001$ for comparisons of control and experimental distributions on day 20 in both high- and low-tide situations). The third species, *N. ziczac,* moved upwards in the absence of the other species of gastropods, although the day-20 difference between control and experimental distributions was only significantly different in the low-tide situation ($P < 0.01$), and not in the high-tide situation ($P = 0.08$). There was no evidence for a general broadening of distribution in the absence of potential competitors. This is shown by the general similarity of the histograms between day-1 and day-20 situations for a given species. The second major point to be noted from the data presented in Figures 1–3

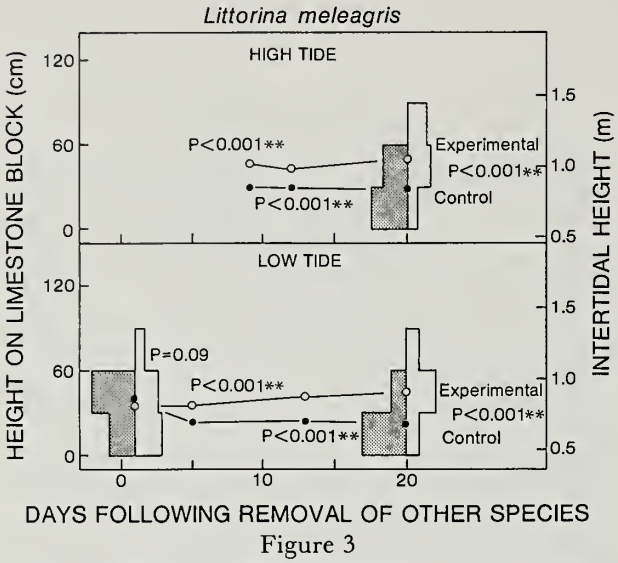

Figure 3

Temporal changes in distributional patterns of *Littorina meleagris* at high and low tides on limestone blocks in Barbados, W.I. Each point represents the mean of 70–159 animals for the high-tide curves and 54–184 animals for the low-tide curves. Probability levels (one-tailed format) are determined from the Mann-Whitney U statistic calculated from the total distribution represented by each mean value. Other details as specified for Figure 1.

is that, with some exceptions, the positions occupied by these littorinid species changed between high and low tides. Thus, in all instances save the *N. ziczac* experimental group (Figure 2) the animals moved upwards at high tide (considering the day-20 positions only; differences, however, were significant at $P = 0.05$ for only *N. tuberculata,* experimental and control groups, and *L. meleagris,* control group; Mann-Whitney U test). At the same time there appeared to be no discernible change in the pattern of distribution of any of the littorinid species between spring- and neap-tide series. This may have been because the wave swash, extending almost the full height of the block (2.25 m above MLLW) on even moderate daily tides, would have obliterated such tidal effects. Change in abundance of a littorine species in response to absence of a possible competing species was not specifically investigated in this study. However, based on visual comparison of day-1 and day-20 histogram widths indicating numbers of littorines in 30-cm band heights for a given species (Figures 1–3), survivorship was good in all plots.

Limpet-Littorine Interactions

On the lowest part of the limestone blocks (0.45–1.00 m above MLLW) the distribution of the limpet *Acmaea jamaicensis* closely overlapped the distribution of the smallest littorine *Littorina meleagris.* Competitive interactions could include space, as both species preferentially occupied depressions in the limestone blocks, or food, or both.

To assess whether competitive interactions between *Acmaea jamaicensis* and *Littorina meleagris* were occurring, nearest-neighbor techniques were employed (Clark & Evans, 1954) in the following situations: (1) in the absence of limpets, (2) in the absence of littorines (only *L. meleagris* is present at this low-intertidal level), (3) where limpets were present in twice their original abundance, (4) where littorines were present in twice their original abundance, and (5) in a control area where each species was present in its original abundance. The nearest-neighbor method as employed here involved measuring distances from given individuals to their nearest-neighbors (conspecifics), and allowed the degree of aggregation or spacing of the population to be estimated.

The study was conducted on the second of the limestone blocks. Five areas of roughly 36 × 38 cm were delineated and each area separated from the next by a 2-cm wide

Table 1

Summary of nearest-neighbor data for populations of the limpet *Acmaea jamaicensis* and littorine *Littorina meleagris* under the control and experimental conditions shown. The statistic R is the ratio of mean nearest-neighbor distances observed, to mean nearest-neighbor distances expected, in an infinitely large random distribution. P indicates the probability of there being no difference between the observed spacing and randomness (F-test of variance ratios).

	Acmaea jamaicensis				*Littorina meleagris*			
Condition	Observed nearest-neighbor distances, $\bar{x}$ cm	Theoretical expected nearest-neighbor distances, $\bar{x}$ cm	R	P	Observed nearest-neighbor distances, $\bar{x}$ cm	Theoretical expected nearest-neighbor distances, $\bar{x}$ cm	R	P
Control	4.3	4.2	1.02	0.86	4.0	5.0	0.80	0.16
Limpets absent	—	—	—	—	3.1	5.3	0.58	<0.01
Littorines absent	3.0	3.3	0.91	0.36	—	—	—	—
Twice limpet density	2.8	2.6	1.08	0.52	4.0	4.6	0.87	0.36
Twice littorine density	3.5	3.7	0.95	0.70	2.1	3.6	0.58	≪0.001

border cleaned of all organisms. Plots were randomly assigned and densities adjusted based on numbers of each species present in the control plot. Some variation in numbers occurred in the 2-day period between the time of initial adjustment of densities and when the nearest-neighbor data were recorded. However, as no plot showed differences exceeding 15% of the assigned density over the two days, this variation was considered acceptable. The nearest-neighbor data were recorded at low tide from all animals in each plot. Measurements were taken from the apex of each limpet or from the center of the largest shell whorl of each littorine.

Table 1 gives the response of each species, measured as mean nearest-neighbor distances, to (1) the absence of the other species, (2) twice the original density of the other species, and (3) control conditions. The statistic R, the ratio of the mean nearest-neighbor distances observed to the mean nearest-neighbor distances expected in an infinitely large random distribution of a particular density, provides a measure of degree of aggregation (Clark & Evans, 1954). Where distributions are random, $R = 1$; where distributions are maximally aggregated, $R = 0$; and where distributions are maximally spaced, $R = 2.1491$. In the present study the limpets were distributed randomly in the control plot ($R = 1.02$, $P = 0.86$, F-test) and in all experimental plots (R values of 0.91, 1.08, and 0.95 under conditions where littorines were absent, where limpets were in twice their original density, and where littorines were in twice their original density, respectively). An ANOVA showed no significant differences between degree of spacing in these four limpet populations ($P > 0.50$). In contrast, the littorines responded to differences in density of the limpets by tending to disperse more widely under conditions of higher limpet-to-littorine densities (R values of 0.80 and 0.87 in the control plot and twice-limpet-density plot, respectively; these values, however, were not significantly different from random, $\alpha = 0.05$; see Table 1), and tending to aggregate more closely under conditions of lower limpet-to-littorine densities (R value of 0.58 for each of "limpets-absent" plot and "twice-littorine-density" plot; $P < 0.01$ and $\ll 0.001$, respectively). However, an ANOVA to test for differences in nearest-neighbor spacing in these four populations of littorines showed no significance ($P > 0.50$).

In summary, then, studies on intraspecific spacing in these limpet and littorine populations showed that the limpets were behaving independently of the littorines, while the littorines were tending to aggregate more when densities of limpets were lower, and tending to disperse more when densities of limpets were higher (noting that differences from randomness were not significant for the littorines).

Survival of Littorines in Air

Only one of the three littorinid species studied, *Littorina meleagris,* lives in the intertidal zone; the other two species live in the supratidal area of the shore. Thus, in theory, while *L. meleagris* would be exposed to air some 90% of the time (as calculated from tidal charts for the 20-day study), the higher-dwelling species, *Nodilittorina tuberculata* and *N. ziczac,* would spend all of their time in air. In fact, wave action and spray wets all three species during most high tides. Only on extreme low tides, where the force of the waves is dissipated by the protective beachrock platform lying in front of the limestone blocks, would the three littorinid species be fully exposed to air.

Survival of the three species of littorines in dry air was measured by keeping animals in a 30-cm diameter desiccating flask over $CaCl_2$ and removing samples of each species at periodic intervals to test for recovery in seawater. For convenience in handling and to ensure that the snails did not clump together or change their orientation after placement in the flask, they were attached to standard glass microscope slides in sets of 10 of each species. Each animal was secured with plasticine at the largest shell whorl such that the snail was positioned with its aperture facing downwards onto the glass slide. The snails were arrayed on each slide in two evenly spaced rows of five. The size range of each species corresponded to average adult size, and snails were selected within as narrow a range as possible. The size ranges chosen were 11–13 mm (shell height) for *Nodilittorina tuberculata,* 10–12 mm for *N. ziczac,* and 5–6 mm for *Littorina meleagris.* Temperatures in the desiccator ranged from a maximum of 31°C during the day to a minimum of 26°C at night. Humidity was not measured, but was considered to be close to zero in the flask. At 3-day intervals (or slightly longer in a few instances) a microscope slide with its attached animals, one slide for each species, was removed from the flask. The animals were gently released from their mucus fastenings and placed in fresh seawater at room temperature (28°C). After 24 h the number of each species alive was recorded. When it was discovered that the lowermost intertidal species *L. meleagris* suffered almost 100% mortality in the first 3-day period, the procedure for this species was modified to test sets of animals at 8-h intervals over a 72-h period.

Figure 4 shows the percentage survival of each species in the desiccator flask. After 32 and 31 days the two supratidal species *Nodilittorina tuberculata* and *N. ziczac* had suffered about 25 and 75% mortality, respectively. In comparison, the lower-dwelling intertidal species *Littorina meleagris* had suffered almost 100% mortality in 3 days. The experiment was terminated after 32 days.

It should be noted that a second experiment, namely testing survival of fully immersed animals, produced no mortality in any of the three species over a 2-week period.

Comparative Ctenidial Morphology of the Three Littorinids

Initial observations of the mantle cavity of the three littorinids showed differences in the ctenidium structure which extends across the roof of the mantle cavity (Figure

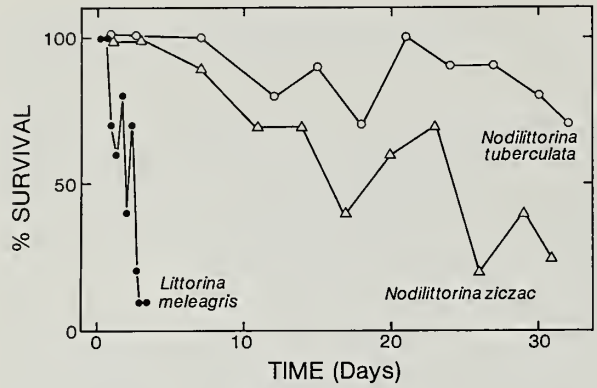

Figure 4

Percentage survival of *Nodilittorina tuberculata, N. ziczac,* and *Littorina meleagris* in dry air at 26–31°C. Each point represents the percentage of a set of 10 animals still alive after a 24-h recovery period in seawater.

5). Whole-mounts of individual ctenidial filaments taken from the broadest region of the ctenidium showed that in all three species there was a triangular region lateral to and left of the efferent branchial vessel where the epithelium consists of ciliated cells interspersed among cells exhibiting secretory activity (Figure 5). The latter are presumably mucus-producing cells, and this region of the ctenidium is thought to function in moving a water current across the surface of the ctenidium as well as in trapping and removing suspended matter entering the mantle cavity, as occurs in a wide variety of gastropods with aquatic gaseous exchange (Fretter & Graham, 1962). In *Littorina meleagris,* the entire ctenidium exhibits this cellular structure, while in *Nodilittorina ziczac* and *N. tuberculata,* two regions can be distinguished in the ctenidium: a row of triangular filaments as described above (Figure 5) and, extending from this region, a row of sickle-shaped filaments spanning the mantle roof. The ventral surface of the latter region in both species is vascularized, and ciliated and secretory cells are absent. This part of the ctenidium is presumably important in aerial respiration.

To quantify these observed morphological differences, 21–23 specimens were selected from each species to include the entire size range of the population. These were anaesthetized in a 10% w/v solution of $MgCl_2$ in seawater for 24 h, then killed in the relaxed state by slow addition of 8% seawater-formalin solution to the narcotizing fluid. They were preserved in formalin, decalcified in a 10% solution of nitric acid, and then washed in three changes of distilled water. The ciliated and non-ciliated (if present) components of each ctenidium were carefully dissected out, and these two parts and the rest of the body were dried separately to constant weight at 80°C, and weighed.

The relationships between dry weights of the two ctenidial components and total shell-free dry body weight for the three species are shown in Figures 6 and 7. It is apparent that *Littorina meleagris* has the largest relative ciliated gill weight (dry weight of ciliated gill : dry weight of shell-free body) and thus, presumably, the greatest surface area of this component (here considered as an organ for aquatic gaseous exchange). Differences in relative ciliated gill weights and relative non-ciliated gill weights were tested between species pairs using a Mann-Whitney U test, with results shown in Table 2. From these results we conclude, (1) that *L. meleagris* differs from the other two littorinid species in having a significantly larger relative ciliated gill weight ($P < 0.001$ for comparisons of *L. meleagris* with each of the other two species; Table 2), (2)

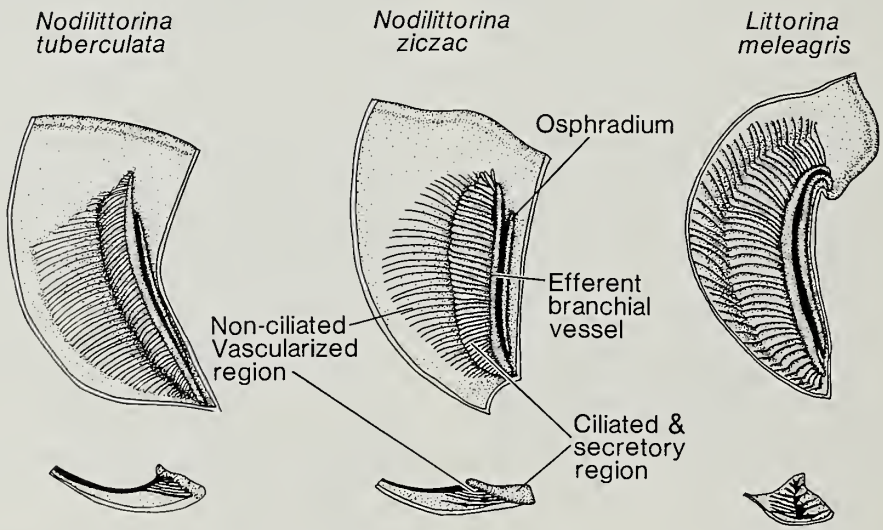

Figure 5

The morphology of the mantle roof of *Nodilittorina tuberculata, N. ziczac,* and *Littorina meleagris,* with detail of a ctenidial filament of each species taken from the broadest region of the ctenidium.

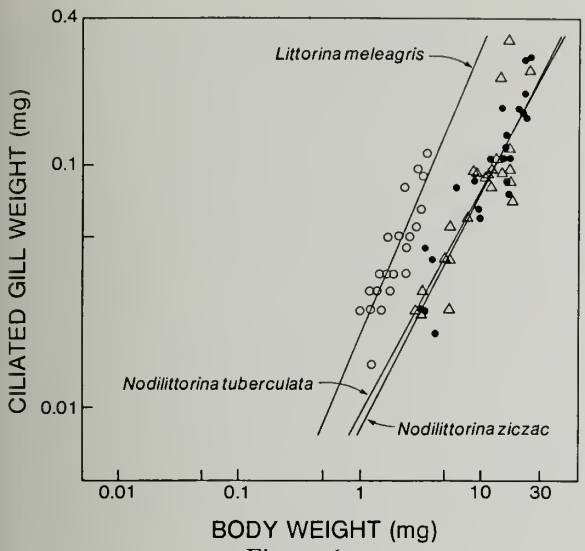

Figure 6

The relationship between ciliated gill dry weight and whole body dry weight in *Nodilittorina tuberculata* (n = 23, closed circle), *N. ziczac* (n = 23, triangle), and *Littorina meleagris* (n = 21, open circle). Equations of regressions, $\log Y = \log a + b \log X$: *N. tuberculata:* $\log a = -2.0365$, $b = 0.9372$, $r = 0.91$; *N. ziczac:* $\log a = -2.0930$, $b = 0.9736$, $r = 0.86$; *L. meleagris:* $\log a = -1.7104$, $b = 1.1799$, $r = 0.87$. All slopes are significantly different from 0 ($P < 0.001$).

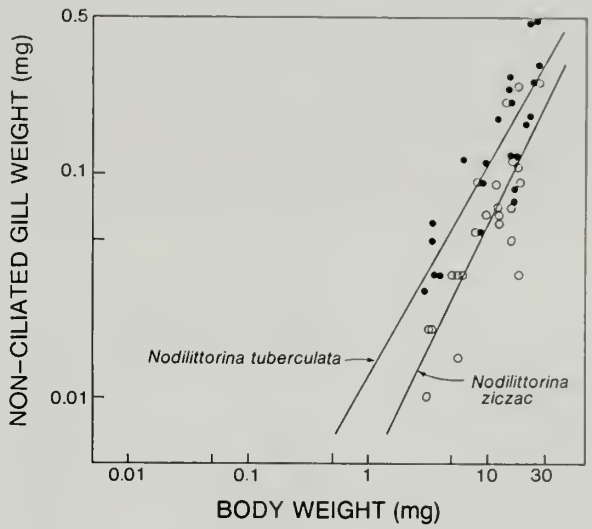

Figure 7

The relationship between non-ciliated gill dry weight and whole body dry weight in *Nodilittorina tuberculata* (n = 23, closed circle) and *N. ziczac* (n = 23, open circle). Equations for the regressions, $\log Y = \log a + b \log X$: *N. tuberculata:* $\log a = -1.9228$, $b = 0.9586$, $r = 0.84$; *N. ziczac:* $\log a = -2.3597$, $b = 1.1289$, $r = 0.83$. Both slopes are significantly different from 0 ($P < 0.001$).

that there are no significant differences between *Nodilittorina tuberculata* and *N. ziczac* with respect to the ciliated component of the ctenidium ($P > 0.50$), and (3) that *N. tuberculata* has a significantly larger relative non-ciliated gill weight compared to *N. ziczac* ($P < 0.001$).

DISCUSSION

Vertical distribution patterns of intertidal gastropods are regulated by a number of environmental factors. Interspecific competition, resistance or tolerance to desiccation and immersion, and morphological variation in relation to possible differential modes of gaseous exchange have been investigated in this study. We have assumed that in the absence of interspecific competition, each of the three littorinid species would occupy a "preferred" intertidal zone, the height and dimensions of which would be determined by other environmental constraints. Hence, any changes in distributional patterns resulting from removal of other littorinid species living in the same environment may have been indicative of interspecific competition.

Apart from the case of *Nodilittorina ziczac* at high tide, all experimental manipulations yielded significantly different distributional patterns in the littorines after a 20-day period. The observed differences occurring at low tide could imply that species were competing for shelter sites. Displacement at high tide, on the other hand, could imply that competition was arising from activities such as feeding, either through species interfering with one another during foraging excursions or competing for actual food items. Removal experiments carried out on the limpet species-pairs *Collisella paradigitalis* (=*Lottia strigatella*) and *C. digitalis* (=*Lottia digitalis*) (CHOAT, 1977), and *C. digitalis* and "*Collisella*" *scabra* (HAVEN, 1973) resulted in displacement and differential growth rates, respectively, demonstrating in the first instance, at least, that similar competitive processes may have been occurring in these limpets as in our tropical littorines. In addition, our analyses of nearest-neighbor distances for *Littorina meleagris* and *Acmaea jamaicensis* suggested that the pattern of dispersion in the former species was responsive to manipulation of the densities of the latter.

While the present study has indicated possible effects of interspecific competition on distribution, the lack of replication in the experiments must be kept in mind. Position effects on the block, and possible fence effects and border interactions, could all have influenced the results. Also, little information is provided on the resource or resources for which the sympatric species may be competing. Additionally, while our experiments on the three littorinids demonstrate a displacement in vertical patterns of distribution, the effects of the manipulations on the dispersal of the species-pair *Acmaea jamaicensis* and *Littorina meleagris* indicate that other interactions may be occurring. In this regard, SCHOENER (1983) found the traditional classification of competition into "exploitative" and "interference" types unsatisfactory, and proposed a new division into six classes. Of these, "overgrowth" competition may be ignored in this study, as all species under investigation were motile. There was also no evidence of "chemical"

Table 2

Ratio of dry gill weight to dry body weight in the littorines *Nodilittorina tuberculata, N. ziczac,* and *Littorina meleagris,* with values of *Z* indicated for Mann-Whitney U tests on each species pair. Statistics for both ciliated and non-ciliated portions of the gills are shown.

Species	Dry gill weight: dry body weight	*Z* value (Mann-Whitney U test)		*P*
Ciliated				
Nodilittorina tuberculata	0.0083	0.52		>0.50
N. ziczac	0.0081		5.62	<0.001
Littorina meleagris	0.0227	5.50		<0.001
Non-ciliated				
N. tuberculata	0.0118	3.90		
N. ziczac	0.0065			<0.001

competition, as individuals of different species were observed to touch one another without any apparent escape or urticating reactions being elicited. There is a strong possibility that "preemptive" (passive occupation of space) and/or "consumptive" (consumption of a common food) competition may occur among the four species examined in this study, and the nearest-neighbor information obtained for *A. jamaicensis* and *L. meleagris* indicate the further possibility of "territorial" and "encounter" competition as defined by SCHOENER (1983). The basis for this conjecture is that while *A. jamaicensis* in high densities tended to increase intraspecific dispersal in *L. meleagris,* a reciprocal effect was not noted. Casual observations on 14 marked *A. jamaicensis* occupying identified resting sites at low tide indicated that 11 of them remained in the same position at low tide after a period of three days. This suggests that if these individuals had been foraging for food during that period, 79% had returned to a "home" site. Territorial defense of home ranges has been recorded for the acmaeid limpets "*Collisella*" *scabra* (SUTHERLAND, 1970) and *Lottia gigantea* (STIMSON, 1973) and for the pulmonate limpet *Siphonaria kurracheensis* (BLACK, 1979). A similar process in *A. jamaicensis* could account for the apparent random distribution of this species regardless of its own density, and for the unilateral influence of this species on *Littorina meleagris,* for which territorial behavior was not apparent.

While all four species under investigation were grazing on algae, some degree of specialization was apparent in *Nodilittorina tuberculata* which consumed mostly a thick-walled unicellular alga inhabiting the high intertidal levels. There was no further evidence of food partitioning among the four species. Thus, had food become a limiting factor, competition should have occurred. The shift in distributional patterns occurring between experimental and control snails at high tide unfortunately provides no direct evidence for either an interference type of competition, perhaps during feeding excursions, or an exploitative type of competition for common food resources.

While competitive effects were demonstrated amongst these four species of gastropods, changes in vertical distribution following the removal of competitively dominant species were not as large as might be predicted on the basis of the amount of space made available ("preemptive" competition), and presumably food made available ("consumptive" competition). Thus, in the absence of competitors, neither species of *Nodilittorina* descended to the lowest level of the experimental block, despite the greater variety of food there. Furthermore, *Littorina meleagris* only moved upwards 30 cm in the absence of the other species and thus did not occupy all the available space. Our findings apparently contrast those of DAYTON (1971), MENGE (1976), and others in studies of temperate rocky shores where space has been demonstrated to be a limited resource.

Predation has been shown to influence the lower limits and patterns of distribution in a number of intertidal species (CONNELL, 1961; PAINE, 1971, 1974; LUBCHENCO & MENGE, 1978; MENGE, 1976; GARRITY & LEVINGS, 1981) and the possibility that *Nodilittorina tuberculata* and *N. ziczac* were similarly regulated cannot be ignored. In this regard, HAMILTON (1976) suggested that upshore migration of *Littorina irrorata* was an escape reaction to predation by the portunid crab *Callinectes sapidus,* and MCQUAID (1982) proposed that the gastropod *Oxystele variegata* migrated upshore to the degree that its tolerance to aerial exposure would allow as an escape response to predation by the whelk *Burnupena delalandii.* In the Six Men's Bay study area, species closely related to those commonly identified as predators of *Littorina* spp. (see PETTITT, 1975) were either not present or occurred only sporadically. For example, three species of *Thais* (Muricidae) recorded in LEWIS' (1960) faunal description of western Barbados coasts were rarely encountered. Although predation by fishes at high tide was a strong possibility (MCCORMACK, 1982), the dominant presence of *L. meleagris,* a much smaller and softer-shelled species, in the lowest intertidal level of the experimental block provided circumstantial evidence that predation by fish at high tide was unlikely to be of major importance. Furthermore, the downward migration of *N. tuberculata* after experimental manipulation did not result in a significant progressive reduction in numbers within the total plot area throughout the course of the experimental period, which was to be expected if downward migration resulted in increased susceptibility to predation at high tide.

The apparent avoidance by *Nodilittorina tuberculata* of low intertidal regions may have been related to a preference for unicellular algae (comparatively less abundant in the lower intertidal regions) or to a greater reliance by this species on an aerial mode of oxygen uptake. Examination of the mantle cavity revealed that both of the higher level

species *N. tuberculata* and *N. ziczac* had two components making up the ctenidium, apparently adapted to each of aerial and aquatic gaseous exchange, respectively (Figure 5). (In comparison, the lowermost species *Littorina meleagris* lacked the non-ciliated or aerial portion of the gill entirely.) This morphological development may have limited the degree of aquatic gaseous exchange in these uppermost species, leading to an avoidance of lower shore levels and the associated long periods of immersion. Although periods of immersion of 14 days did not result in death in any of the species, the condition of the animals was not monitored. Further research would be needed to examine the degree of differential reliance on aerial and aquatic respiration in these littorinid species.

Our investigation on zonation patterns of the three species of littorinids accords with BANDEL's observations (1974) on the same species from a number of sites in the Atlantic. This consistency in zonation pattern, together with data presented here showing an increased tolerance to desiccation, as well as a tendency for morphological modifications in the mantle cavity in those species occupying high intertidal levels, indicate that physical stresses associated with aerial exposure may limit upper distribution. VERMEIJ (1973) also found morphological gradients in increased shell sculpture and relative spire height among intertidal tropical littorinids as intertidal heights increased, and considered that these features increased the snails' tolerance to water loss and heat stress associated with their high intertidal life. However, if as WOLCOTT (1973) has hypothesized, intertidal gastropods are invariably zoned just below the limits of their tolerance to various environmental factors, then deaths resulting from such stresses that act to limit upper distributions of a species may occur only rarely. Each of the three littorinids tested in the present study showed tolerance to desiccating circumstances that exceeded the tolerance required for survival in the uppermost region of their distribution. Thus, wave splash on the experimental block would ensure that *Littorina meleagris* would experience exposure to air for only brief periods during each tide, while both species of *Nodilittorina* would experience wetting at least during spring tides, the intervals between these being considerably shorter than that required to achieve significant mortality in the laboratory experiment (Figure 4). While these results offer some support to the notion that desiccation may be setting upper limits of distribution of these tropical littorinids, especially for *L. meleagris,* we must heed UNDERWOOD's (1979) caution that field experiments are necessary to establish firmly the critical limits of tolerance of a species to physical stresses.

Much information is currently available on the structuring of intertidal communities on temperate shores, particularly on the interplay between the relative importance of physical factors and various biological factors, such as predation and competition (*e.g.,* DAYTON, 1971; CONNELL, 1961, 1975; MENGE, 1976; BLACK, 1979). However, there are fewer comparable reports on tropical littoral systems, especially with regard to long-term studies on competition (see LEVINGS & GARRITY, 1983). Owing to significant differences in physical and biological properties between temperate and tropical systems (see BRANCH, 1976; GARRITY, 1984), generalizations made on the basis of studies in one may not apply to the other, and more research will be needed to unravel the role that competition plays in the structuring of intertidal systems in the tropics.

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LITERATURE CITED

BANDEL, K. 1974. Studies on Littorinidae from the Atlantic. Veliger 17:92–114.

BLACK, R. 1979. Competition between intertidal limpets: an intrusive niche on a steep resource gradient. Jour. Anim. Ecol. 48:401–411.

BRANCH, G. M. 1975a. Intraspecific competition in *Patella cochlear* Born. Jour. Anim. Ecol. 44:263–281.

BRANCH, G. M. 1975b. Mechanisms reducing intraspecific competition in *Patella* spp.: migration, differentiation and territorial behaviour. Jour. Anim. Ecol. 44:575–600.

BRANCH, G. M. 1976. Interspecific competition experienced by South African *Patella* species. Jour. Anim. Ecol. 45:507–529.

CHOAT, J. H. 1977. The influence of sessile organisms on the population biology of three species of acmaeid limpets. Jour. Exp. Mar. Biol. Ecol. 26:1–26.

CLARK, P. J. & F. C. EVANS. 1954. Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology 35:445–453.

CONNELL, J. H. 1961. Effects of competition, predation by *Thais lapillus,* and other factors on natural populations of the barnacle *Balanus balanoides.* Ecol. Monogr. 31:61–104.

CONNELL, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais.* Ecol. Monogr. 40:49–78.

CONNELL, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pp. 460–490. *In:* M. L. Cody and J. M. Diamond (eds.), Ecology and evolution of communities. Harvard University Press: Cambridge, Massachusetts.

CREESE, R. G. 1982. Distribution and abundance of the acmaeid limpet, *Patelloida latistrigata.* Oecologia 52:85–96.

CREESE, R. G. & A. J. UNDERWOOD. 1982. Analysis of inter- and intra-specific competition amongst intertidal limpets with different methods of feeding. Oecologia 53:337–346.

DAYTON, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization

of space in a rocky intertidal community. Ecol. Monogr. 41: 351–389.

FRETTER, V. & A. GRAHAM. 1962. British prosobranch molluscs. Ray Society: London. 755 pp.

GARRITY, S. D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. Ecology 65:559–574.

GARRITY, S. D. & S. C. LEVINGS. 1981. A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods: direct, indirect and community effects. Ecol. Monogr. 51:267–286.

HAMILTON, P. V. 1976. Predation on *Littorina irrorata* (Mollusca: Gastropoda) by *Callinectes sapidus* (Crustacea: Portunidae). Bull. Mar. Sci. 26:403–409.

HAVEN, S. B. 1973. Competition for food between the intertidal gastropods *Acmaea scabra* and *Acmaea digitalis*. Ecology 54: 143–151.

KOHN, A. J. 1959. The ecology of *Conus* in Hawaii. Ecol. Monogr. 29:47–90.

LEVINGS, S. C. & S. D. GARRITY. 1983. Diel and tidal movement of two co-occuring neritid snails; differences in grazing patterns on a tropical rocky shore. Jour. Exp. Mar. Biol. Ecol. 67:261–278.

LEWIS, J. B. 1960. The fauna of rocky shores of Barbados, West Indies. Can. Jour. Zool. 38:391–435.

LINDBERG, D. R. 1986. Name changes in the "Acmaeidae." Veliger 29:142–148.

LUBCHENCO, J. & B. A. MENGE. 1978. Community development and persistence in a low rocky intertidal zone. Ecol. Monogr. 48:67–94.

MCCORMACK, S. M. D. 1982. The maintenance of shore-level size gradients in an intertidal snail (*Littorina sitkana*). Oecologia 54:177–183.

MCQUAID, C. D. 1982. The influence of desiccation and predation on vertical size gradients in populations of the gastropod *Oxystele variegata* (Anton) on an exposed rocky shore. Oecologia 53:123–127.

MENGE, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecol. Monogr. 46:355–393.

PAINE, R. T. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology 52:1096–1106.

PAINE, R. T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93–120.

PETTITT, C. 1975. A review of the predators of *Littorina*, especially those of *L. saxatilis* (Olivi) (Gastropoda: Prosobranchia). Jour. Conch. 28:343–357.

SCHOENER, T. W. 1983. Field experiments on interspecific competition. Amer. Natur. 122:240–285.

STIMSON, J. 1973. The role of the territory in the ecology of the intertidal limpet *Lottia gigantea* (Gray). Ecology 54:1020–1030.

SUTHERLAND, J. P. 1970. Dynamics of high and low populations of the limpet, *Acmaea scabra* (Gould). Ecol. Monogr. 40:169–188.

UNDERWOOD, A. J. 1976. Food competition between age-classes in the intertidal neritacean *Nerita atramentosa* Reeve (Gastropoda: Prosobranchia). Jour. Exp. Mar. Biol. Ecol. 23: 145–154.

UNDERWOOD, A. J. 1978. An experimental evaluation of competition between three species of intertidal prosobranch gastropods. Oecologia 33:185–202.

UNDERWOOD, A. J. 1979. The ecology of intertidal gastropods. Adv. Mar. Biol. 16:111–210.

VERMEIJ, G. J. 1973. Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. Mar. Biol. 20:319–346.

WOLCOTT, T. G. 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at "limiting factors." Biol. Bull. 145:389–422.

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Patch Formation by the Ectoparasitic Snail *Boonea impressa* on Its Oyster Host, *Crassostrea virginica*

by

E. A. WILSON, M. E. WHITE,[1] E. N. POWELL

Department of Oceanography, Texas A&M University,
College Station, Texas 77843, U.S.A.

AND

S. M. RAY

Department of Marine Biology, Texas A&M University at Galveston,
Galveston, Texas 77550, U.S.A.

Abstract. *Boonea impressa* (=*Odostomia impressa*) is a common ectoparasite of the oyster *Crassostrea virginica*. Snail populations are contagiously distributed. Studies were conducted to determine what factors influence patch formation of *B. impressa* in oyster populations. Physical characteristics of oysters such as orientation, age, size, and level of *Perkinsus marinus* (=*Dermocystidium marinum*) infection did not affect host acceptability in adult snails. Patch formation occurred independently of any tested oyster characteristic. Aggregates usually formed on the clumps nearest where snails were initially placed. Snails moved frequently from host to host, but snails preferentially moved between existing aggregates. Although up to 35% of the population moved daily, patch location remained stable for at least 5 to 6 days. Patches may form through chance meetings during foraging and grow in size as a result of gregarious behavior. Patches were spatially more stable than the individuals that composed them indicating that refugia from snail parasitism may exist in oyster populations. Therefore, the effect of this parasite on its host population may depend more on the spatial and temporal dynamics of the patch than on the parasites themselves.

INTRODUCTION

Movement and patch formation of gastropod populations occur on different temporal and spatial scales depending on the reason for aggregation. Patches form for reproduction, feeding (FEARE, 1971; CATTERALL & POINER, 1983), and protection from physical conditions (HAZLETT, 1984; GARRITY & LEVINGS, 1984), for example. Factors influencing gastropod behavior include season (FEARE, 1971), maintenance of position in the intertidal zone (HAZLETT, 1984), diurnal rhythms, and chemotaxis (RHODE & SANDLAND, 1975). In some cases, factors initiating the aggregation disappear long before the aggregate does (HARTNOLL & HAWKINS, 1985).

The pyramidellid gastropod *Boonea impressa* (=*Odostomia impressa*) is a mobile ectoparasite with an aggregated distribution on its host, the American oyster, *Crassostrea virginica* (POWELL *et al.*, 1987). *Boonea impressa* is numerically abundant in oyster reef communities with numbers reported as high as 100 per oyster (HOPKINS, 1956). Five to 40 snails per oyster occur frequently in Texas bays (WHITE *et al.*, 1984). Although common, information on behavior in pyramidellids is generally lacking. The pyramidellids are considered entirely parasitic, and anatomical data, although rare, support this conclusion (FRETTER & GRAHAM, 1949; FRETTER, 1951). *Boonea impressa* feeds much like a mosquito by piercing the host with a hollow

[1] National Center for Atmospheric Research, Boulder, Colorado 80307, U.S.A.

stylet and sucking the body fluids with a buccal pump (FRETTER & GRAHAM, 1949; FRETTER, 1951; ALLEN, 1958). *Crassostrea virginica* is the preferred host of *B. impressa* but, like other odostomians, it is not entirely host specific (ROBERTSON & ORR, 1961; BULLOCK & BOSS, 1971).

Parasitism by *Boonea impressa* alters the growth, reproduction, and metabolic condition of its host (WARD & LANGDON, 1986; WHITE *et al.*, in press). *Boonea impressa* can transmit an important disease-producing parasite, *Perkinsus marinus* (=*Dermocystidium marinum*) from host to host (WHITE *et al.*, 1987) and increase infection intensity in previously infected hosts. Therefore, *B. impressa* may have an important, detrimental effect on oyster health, community structure, and population dynamics.

Shape, texture, size, age, movement, and chemical substances all influence host selection in parasites (VINSON, 1976). If the host is distributed patchily, parasites may concentrate their search on patches of higher host density or remain in patches for longer periods of time searching for a suitable host (HASSELL, 1982a; WAAGE, 1983; CHANTARASA-ARD *et al.*, 1984). Under certain circumstances, host populations can thereby be regulated (*e.g.*, HUFFAKER *et al.*, 1986; CHESSON & MURDOCH, 1986). The distribution of the effect of snail parasitism on oyster populations is determined by the location and temporal stability of snail patches. Snails are consistently more patchily distributed than their hosts, but the spatial position of snail patches is not uniformly correlated with that of their hosts. Hence the distribution pattern is best described as host-density vague (POWELL *et al.*, 1987). POWELL *et al.* (1987) suggested that most oysters are acceptable hosts so that factors inherent to the host and its distribution have little effect on snail distribution. Snail patches were considered to form randomly, possibly as foraging-time aggregates, and be maintained by a behavioral change to gregariousness, as is frequently the case in insect swarming behavior (OKUBO, 1980).

Whether patches are random occurrences or not and to what degree patches are temporally stable determine the nature of refugia from parasitism in oyster populations and the resulting effect of parasites on the stability of the host population. The purpose of this study was to determine whether characteristics of the oyster population influence patch formation and location in populations of *Boonea impressa* or whether patches form randomly. Oyster characteristics investigated included position, orientation, age, and the presence and infection intensity of *Perkinsus marinus*. That is, we asked the questions, are some oysters more acceptable hosts than others and does differential acceptability affect patch location?

MATERIALS AND METHODS

All snails and oysters used in the studies were collected from reefs in the Copano Bay–Aransas Bay area of the Texas coast (figs. 1 and 2 in POWELL *et al.*, 1987). Experiments were conducted during the summers of 1984 and 1985 at the University of Texas Marine Science Institute at Port Aransas, Texas.

To study patch formation, oysters were arrayed in a circle in trays completely submerged on a flowing sea table. Seawater supplying the sea table was piped directly from Aransas Pass via an intermediate settling chamber to remove larger particulates. The seawater source and drain were upstream and downstream of the tray, respectively, so that seawater flowed unidirectionally across the tray during the experiment. Seawater temperature was 20–22°C. Aeration was unnecessary.

To initiate an experiment, individuals of *Boonea impressa* were added to the center of the circle of oysters. Consequently, all snails were initially equidistant from all oysters. The number of snails on each oyster was counted daily, and the oysters replaced in the same position in the circle. Four preference tests were conducted, examples of which are depicted in Figures 1–7.

(1) Snail preference for hosts in different spatial orientations was tested by placing 12 oysters alternately horizontally (left valve down) and vertically (dorsal edge down) in the circular arrangement depicted in Figure 6. The number of snails on each oyster was recorded daily for 5 days.

(2) Eight adults (5–7 cm in length), eight juveniles (2–3 cm in length), and eight groups of spat (seven per group) were placed in a circular arrangement to ascertain snail preference for oysters of different age and size. Seven spat were used per group so that sufficient feeding space would be available to prevent snail crowding from interfering with patch formation. The number of snails on each oyster or group of spat was recorded daily for 6 days. The snails were then removed, the same oysters randomly rearranged around the circle (as shown in Figure 5), and the same snails placed again in the circle's center. Snail position was recorded for another 4 days.

(3) Snail preferences might involve more subtle cues than host orientation or size. To determine whether patches formed on preferred oysters for any reason or on oysters placed in preferred positions in the circle, adult oysters of approximately equal size were used. Snails were allowed to form patches over a period of days. The snails were then removed and the same oysters rearranged in the circle. The same snails were added a second time and their position recorded each subsequent day. Either preferred oysters or preferred positions could then be identified and further analyzed. Two replicate experiments were run. In the first, eight oysters were arranged in a circle. Snail position was recorded daily for 5 days, the oysters rearranged about the circumference, the same snails added to the center, and their position monitored daily for 5 more days. Finally, the oysters were rearranged a third time, the same snails added again, and their positions monitored again for 5 days. The three different arrangements are shown in Figure 2. In the second experiment, 19 oysters were arranged as shown in Figures 3 and 4. Snail positions were monitored twice daily for 6 days, the oysters randomly rearranged, the same snails again added to the circle's

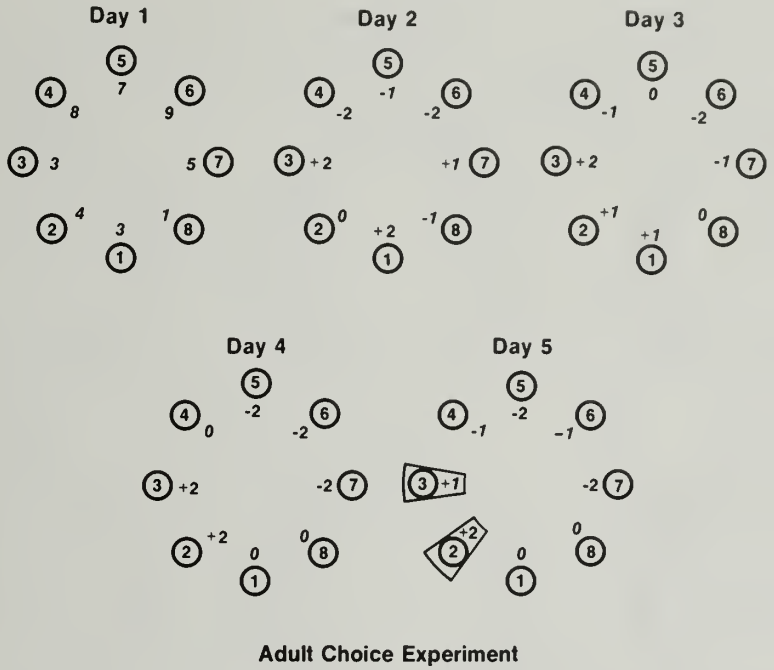

Figure 1

Representative results of snail patch formation on adult oysters. Numbers within circles designate individual oysters (No. 1, No. 2, etc.). Numbers outside circles designate the net number of snails added or lost by that oyster over the previous 24 h, except for day 1 which shows the initial distribution. Rectangled oysters (day 5) indicate location of final aggregates (see Figure 2).

center, and the snail's positions recorded twice daily for another 6 days.

(4) To determine whether snails preferred nearby oysters, 20 oysters were placed randomly on a flooded sea table as shown in Figure 7, and snails added to the center. The number of snails on each oyster was counted once a day for one week.

After the experiments were concluded, each oyster was assayed for the presence and intensity of infection by *Perkinsus marinus* by excising a small piece of mantle tissue and culturing it in thioglycolate medium (Ray, 1966). Infection was determined microscopically after staining with Lugol's solution and the intensity of infection was scored using the semiquantitative 0-to-5-point scale of Mackin (1962).

RESULTS

Representative distributions of snails among oysters are depicted in Figures 1–7. A minimum estimate of the number of snails moving daily can be made by summing the number of snails lost by oysters having fewer snails at the

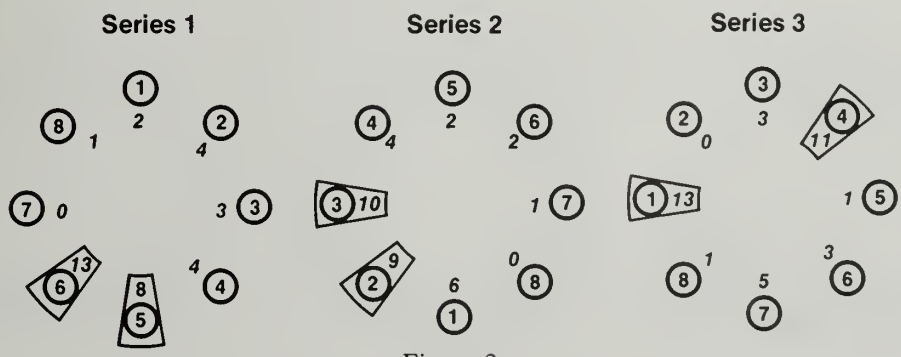

Figure 2

Patch formation of snails on the same adult oysters occupying different positions in the circle (see also Figure 1). The circled numbers designate individual oysters, and the uncircled numbers the number of snails at the end of each series, at which time all snails were removed and all oysters repositioned as described in the Methods Section. Rectangled circles indicate locations of aggregates.

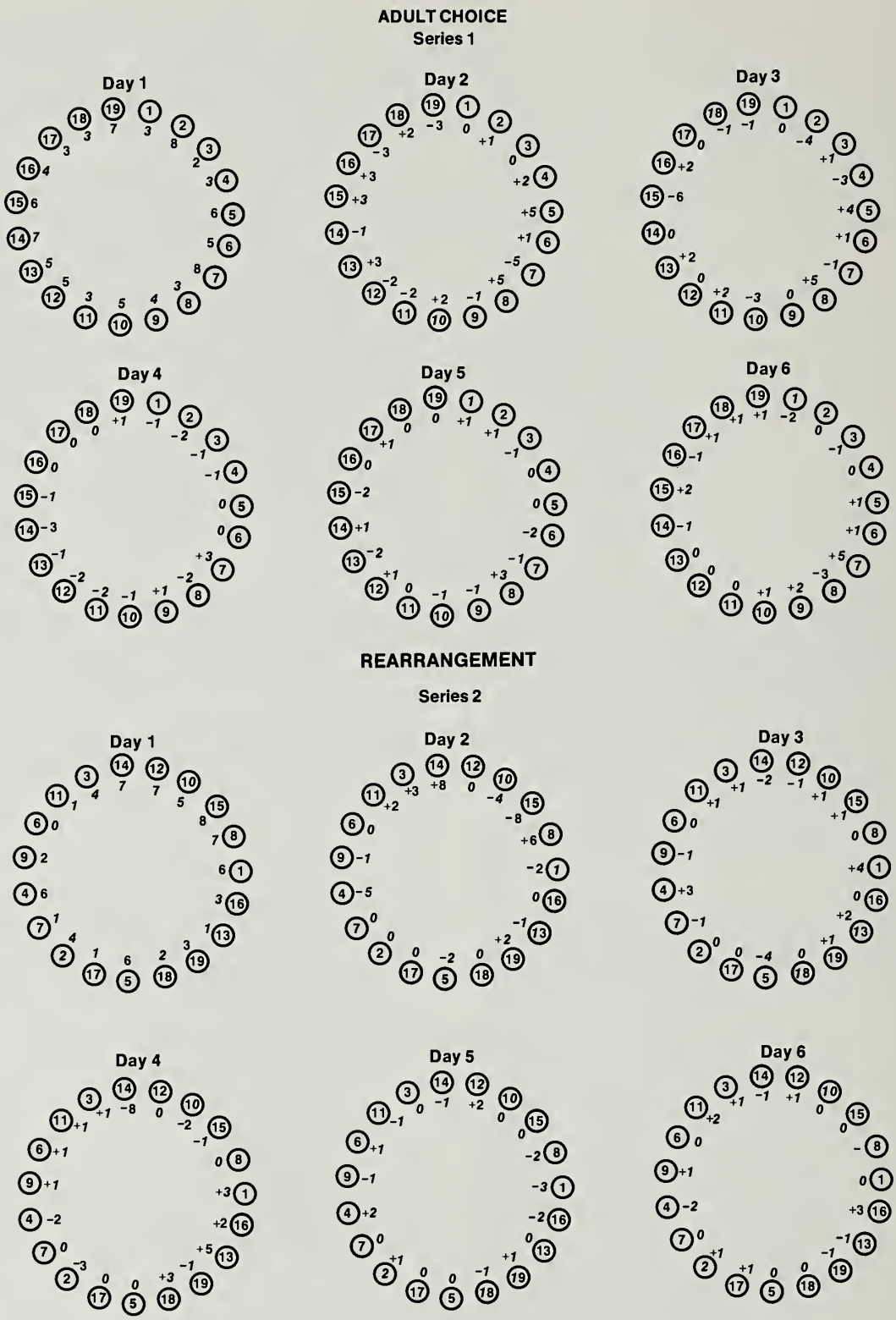

Figure 3

Representative results of snail patch formation on adult oysters (see also Figure 4). Numbers within circles designate individual oysters (No. 1, No. 2, etc.). Numbers outside circles designate the net number of snails added or lost by that oyster over the previous 12 h, except for day 1 which shows the initial distribution.

next daily observation. At least 10–20% of the snails moved each day in experiments where oysters were arranged in a circle. In the experiment where oysters were arranged randomly on the sea table, at least 20–35% of the snails moved each day.

Differences in snail distribution from one observation to the next were assessed by Spearman's rank analysis (Tables 1–5). A significant difference using this test indicates that the two distributions compared were similar to each other. Typically, the longer the experiment went on, the more the initial distribution varied from the final distribution. Usually distributions separated by 3 or more days were no longer similar enough to produce a significant correlation. The significance of contagious (patchy), random, and even distributions were judged using chi-square tests ($\alpha = 0.05$) of I, where $I = s^2/\bar{x}$, as described by ELLIOTT (1977). In all experiments, the snails' final distribution was contagious (Table 6). Snail distribution was frequently random during the initial few days of observation, however. Hence, the distributional pattern became more contagious as the experiment progressed. In general, oysters that had snail aggregates continued to recruit snails from other oysters initially and then maintained a larger number despite continued snail relocation. That is, the number of snails moving daily did not obviously decrease with time during most experiments. Moreover, in most experiments, we used an average of 4 to 6 snails per oyster; yet the maximum number observed on any oyster was only 17. Hence, on the average, snails tended to relocate by moving to and from existing aggregates once the aggregates became established and, after a time, aggregates ceased to grow in size.

To determine whether the location of snail aggregates was really temporally stable or not, we tabulated, for each oyster, the number of observations in which its number of snails was above or below the daily mean for all oysters. If the location of snail aggregates was temporally stable, then the number of times the oyster was observed to be above or below the daily mean should differ significantly from a 50:50 split using the binomial test. The oyster would tend to remain above or below the mean from one observation period to the next. By chance, some oysters may produce significant results. Hence, the number of significant results was itself tested for significance using the same test. Aggregates were judged temporally stable in an experiment when the number of oysters in the experiment that differed significantly from a 50:50 ratio (number of observations above the daily mean : number of observations below the daily mean) was more than would be expected by chance at $\alpha = 0.05$. The results were significant in all cases. In fact, most oysters having less or more snails than the mean on the second day retained that relative position with respect to the mean throughout the remainder of the experiment.

Intensity of infection by *Perkinsus marinus* ranged from uninfected to heavily infected (0 to 5 on Mackin's 1962 scale). With one exception, infection intensity did not significantly correlate with snail distribution on oysters, however (Tables 1–5) (Spearman's rank, $\alpha = 0.05$). There was no significant difference in the number of snails on vertically or horizontally oriented oysters (Table 1, Figure 6) (Mann-Whitney, $\alpha = 0.05$) or on adults, juveniles, or groups of spat (Table 3, Figure 5) (Duncan's multiple range on ranked data, $\alpha = 0.05$).

In the experiments where the same oysters were rearranged into different positions around the circle, the final

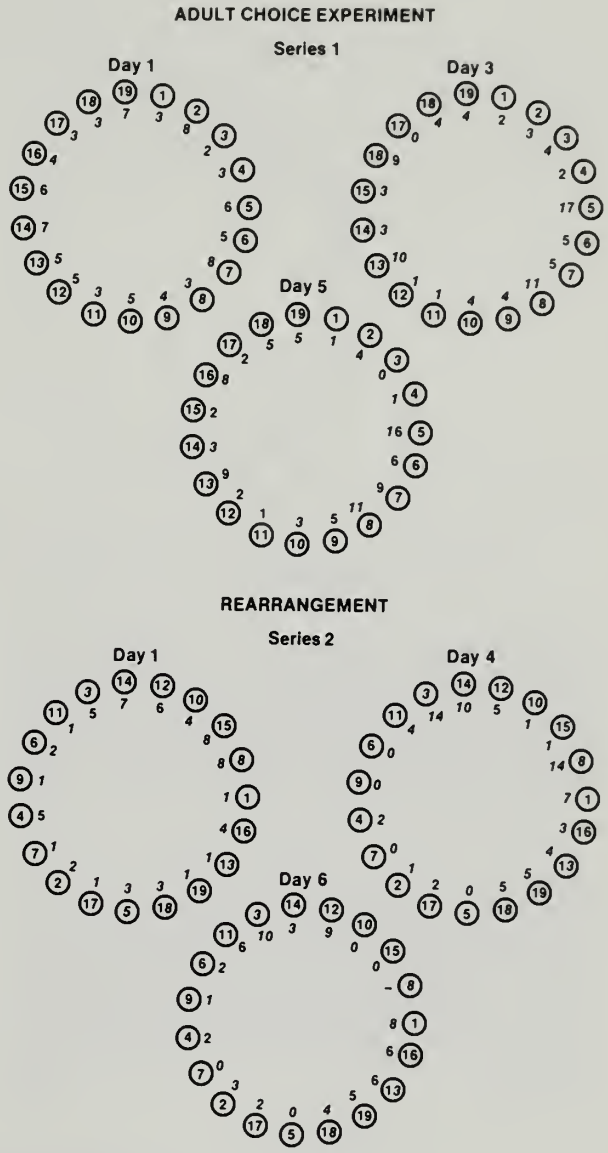

Figure 4

Patch formation of snails on adult oysters occupying different positions in the circle (see also Figure 3). The circled numbers designate individual oysters, and the uncircled numbers the number of snails at the end of each series, at which time all snails were removed and all oysters repositioned as described in the Methods Section.

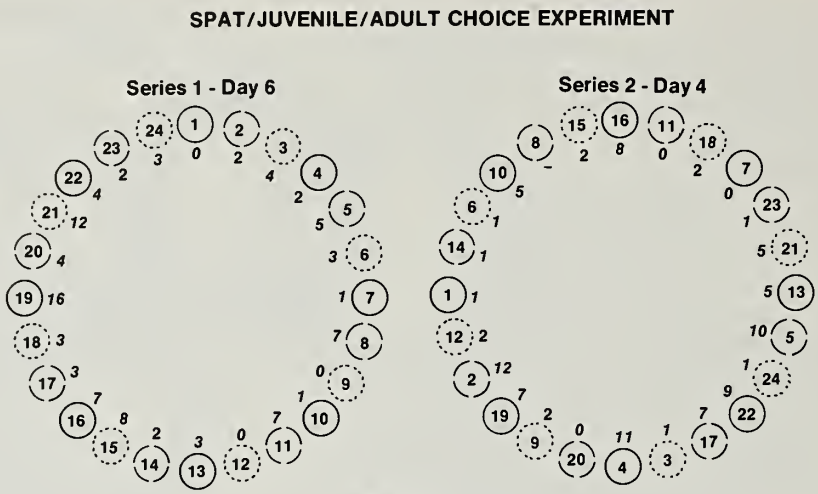

Figure 5

Results of the experiment using oyster adults, juveniles, and groups of spat. Figure layout as in Figure 2. Solid circles, adults; dashed circles, juveniles; dotted circles, spat.

distribution of one series was never correlated with the final distribution of the other (Figures 2, 4, 5) (Spearman's rank, $\alpha = 0.05$). Snails formed aggregates on particular oysters in the first series, and when the oysters were repositioned in the circle, the snails formed aggregates again, but not necessarily on the same oysters.

Moreover, snails were not attracted preferentially to any set of positions on the circle's circumference. In all three experiments where oysters were repositioned, the distribution of snails at the end of the succeeding trial was not significantly correlated with respect to position in the circle with the distribution at the end of the preceeding trial (Figures 2, 4, 5) (Spearman's rank, $\alpha = 0.05$). Hence, snail distribution resulted from intrinsic snail behavior rather than from environmental stimuli or differential host acceptability.

In the experiment where adults, juveniles, and groups of spat were used, the distribution of snails within any one of these three categories in the first series was not significantly correlated with the same distribution in the second (Figure 5). Hence, the observation that aggregates did not form consistently on any particular set of oysters held also for specific size classes.

In one experiment, oysters were distributed on a sea table so that some were farther from the position where snails were added than others (Figure 7). Aggregates formed preferentially on oysters near the position where snails were added even though snails could and did move to the farthest oyster by the end of the first day. These aggregates remained stable throughout the rest of the experiment even though 30% or more of the snails changed positions each day.

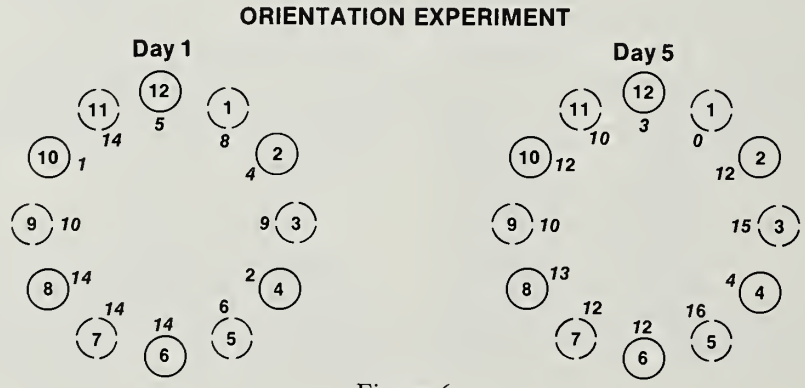

Figure 6

Results of the oyster orientation experiment showing snail positions on first and last day of one experimental series. Figure layout as in Figure 2. Solid circles, horizontal (left valve down) oysters; dashed circles, vertical (dorsal edge down) oysters.

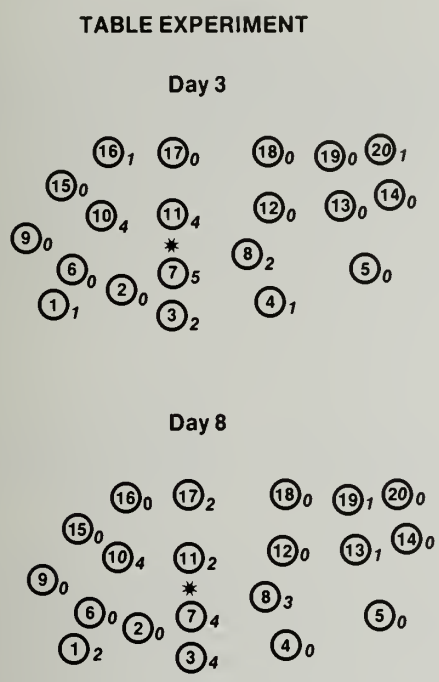

Figure 7

Results of experiment with oysters positioned at various distances from the location (*) where snails were added. Snail positions on days 3 and 8 of the experiment are shown. Figure layout similar to Figure 2. Distance from * to oyster No. 7 is 9 cm.

DISCUSSION

The distribution of parasites on their hosts is an important factor determining the impact of the parasite on the host population (HASSELL, 1982a; ANDERSON & GORDON, 1982). The location of parasite patches can be influenced by a wide variety of factors including host size, shape, and spatial distribution, and the presence of gregarious behavior or interference competition among the parasites (VINSON, 1976; NAGEL & CADE, 1983; WEIS, 1983). *Boonea impressa* did not prefer to aggregate on oysters of a particular size, spatial orientation, or level of infection by *Perkinsus marinus*. Nor were any other intrinsic characteristics of the oysters important in determining snail distribution. In all cases where oysters were used in more than one experimental series, *B. impressa* did not consistently select the same suite of oysters for patch formation. POWELL *et al.*

Table 1

Results of Spearman's rank correlations for snail distributions in the experiment using vertically and horizontally positioned oysters (Figure 6). SC, correlation significant (distributions similar) at $\alpha = 0.05$. Analysis of *Perkinsus* used data on disease intensity for the last day of the experiment only.

	Day				
Day	1	2	3	4	5
1	—				
2	X	—			
3	X	SC	—		
4	X	X	X	—	
5	X	X	X	SC	—
Perkinsus	X	SC	SC	X	X

Table 2

Results of Spearman's rank correlations for snail distributions in the experiment with oysters positioned at various distances from the location where snails were initially added (Figure 7). See Table 1 for further explanation.

	Day							
Day	1	2	3	4	5	6	7	8
1	—							
2	SC	—						
3	X	SC	—					
4	SC	SC	SC	—				
5	X	SC	SC	SC	—			
6	X	SC	SC	SC	SC	—		
7	X	SC	SC	SC	SC	SC	—	
8	X	SC	SC	SC	SC	SC	SC	—
Perkinsus	X	X	X	X	X	X	X	X

Table 3

Results of Spearman's rank correlations for snail distributions where oyster adults, juveniles, and groups of spat were used (Figure 5). SC, correlation significant at $\alpha = 0.05$. Analysis of *Perkinsus* used data on disease intensity for the last day of the last series only.

Series 1

	Day				
Day	1	2	3	4	5
1	—				
2	SC	—			
3	SC	SC	—		
4	SC	SC	SC	—	
5	X	SC	SC	SC	—
Perkinsus	X	X	X	X	—

Series 2

	Day					
Day	1	2	3	4	5	6
1	—					
2	SC	—				
3	SC	SC	—			
4	SC	SC	SC	—		
5	SC	SC	SC	SC	—	
6	SC	SC	SC	SC	SC	—
Perkinsus	X	X	X	X	X	X

Table 4

Results of Spearman's rank correlations for snail distributions in the experiment using only adult oysters (Figures 1–2). See Table 3 for further explanation.

Series 1

	Day				
Day	1	2	3	4	5
1	—				
2	X	—			
3	X	SC	—		
4	X	SC	SC	—	
5	X	SC	SC	SC	—
Perkinsus	X	X	X	X	X

Series 2

	Day				
Day	1	2	3	4	5
1	—				
2	SC	—			
3	X	X	—		
4	X	X	SC	—	
5	X	X	X	SC	—
Perkinsus	X	X	X	X	X

Series 3

	Day				
Day	1	2	3	4	5
1	—				
2	SC	—			
3	SC	SC	—		
4	SC	SC	SC	—	
5	SC	SC	SC	SC	—
Perkinsus	SC	SC	X	SC	SC

Table 5

Results of Spearman's rank correlations for snail distributions in the experiment using only adult oysters (Figures 3–4). See Table 3 forfurther explanation.

Series 1

	Day						
Day	1	2	3	4	5	6	7
1	—						
2	SC	—					
3	X	SC	—				
4	X	SC	SC	—			
5	X	X	SC	SC	—		
6	X	X	X	SC	SC	—	
7	X	X	X	X	X	X	—
Perkinsus	X	X	X	X	X	X	X

Series 2

	Day			
Day	1	2	3	4
1	—			
2	SC	—		
3	SC	SC	—	
4	SC	SC	SC	—
Perkinsus	X	X	X	X

(1987) suggested, from field data on snail distributional patterns, that acceptable oyster hosts must occur frequently in the population. Our data suggest that essentially all oysters are equally acceptable to adult snails. Juvenile snails, of course, are more host-size restricted (POWELL *et al.*, 1987), but these were not used in our experiments.

Initially, aggregates continued recruiting members over time, so that the snails' distribution gradually became more contagious. The number of snails was usually limited, however, to 10–15 snails per oyster. The same maximum densities are typically found in the field (WHITE *et al.*, 1984). When the distributional pattern became contagious, the frequency of snail movement did not decline. We observed that at least 10–20% of the snails moved per day throughout each experimental series. WHITE *et al.* (1984) estimated that, in the field, at least 50% of the snail population moved each week. Our data indicate that this is certainly an underestimate. WHITE *et al.* (1984) argued that physical dislodgment, by waves and currents for example, was an unlikely reason for snail relocation. Our analysis supports this conclusion. Snails moved frequently even in the undisturbed environment of the laboratory.

Frequent snail movement, even after the snails' distribution became contagious, indicates that snails preferentially moved from one aggregate to another. RHODE & SANDLAND (1975), FEARE (1971), HAZLETT (1984), and GERHART (1986), among others, suggested that gastropods can locate other snails through the use of pheromones and mucus trails, thereby forming feeding or reproductive aggregates. Preferential movement between aggregates suggests that *Boonea impressa* may also be attracted by a chemical substance produced by other *B. impressa*.

The position of aggregates remained remarkably stable over periods of 5 days or so in spite of continual relocation by individual snails. FEARE (1971) documented a similar phenomenon for *Nucella lapillus*. POWELL *et al.* (1987) suggested that the locations where patches form might be a random process controlled by chance meetings of snails on oysters and that snails tended to move preferentially to nearby clumps so that aggregates tended to be near other aggregates. In the experiment where oysters were distributed at differing distances from the snail's original position, all aggregates occurred on the nearer clumps. More snails bestrode these clumps initially; snails had a greater chance to meet other snails on these clumps and aggregates formed.

The lengths of time a parasite searches for and remains on a suitable host are important determinants in the stability of parasite-host systems. Parasites may spend a large portion of their time searching for hosts that are distributed patchily in the environment (HASSELL, 1982b; MORRISON,

Table 6

I (ELLIOTT, 1977) for each day for each experiment. Asterisks indicate a significant contagious distribution ($\alpha = 0.05$). All other values were not significantly different from random.

Experiment	Day 1	2	3	4	5	6	7	8	9	10	11	12
Figure 2—Adults												
Series 1	0.78	0.51	0.32	1.89	3.95*							
Series 2	1.34	0.84	0.79	1.45	3.92*							
Series 3	0.59	1.57	1.75	2.22*	4.43*							
Figure 4—Adults												
Series 1	0.68	0.91	1.62*	2.36*	2.89*	3.41*	3.46*	3.94*	3.82*	3.14*	3.30*	
Series 2	1.75*	1.59	2.00*	4.41*	4.51*	4.13*	3.98*	3.60*	2.75*	2.98*	4.16*	2.62*
Figure 5—Adult, juvenile, spat	0.88	1.47	1.27	2.19*	3.87*	3.42*	2.03*	2.87*	3.04*	3.54*		
Figure 6—Orientation experiment	3.60*	1.75*	2.61*	2.19*	2.27*							
Figure 7—Distance experiment	1.73*	3.08*	2.23*	2.79*	3.41*	2.95*	3.19*	1.93*				

1986). POWELL *et al.* (1987) showed that *Boonea impressa* is more patchily distributed than its host on natural reefs. Optimal time allocation by the parasite would involve preferential searching in areas of high host density (WAAGE, 1983) because the efficiency of the parasite is partially determined by the time it takes moving between hosts (WEIS, 1983). Feeding cannot occur during this time. For *B. impressa,* reduced mobility once patches have formed would seem to maximize foraging efficiency. Curiously, *B. impressa* does not seem to minimize searching time but instead spends a large amount of time moving from aggregation to aggregation.

SUTHERLAND (1983) suggested that interference among parasites forces some to leave aggregations in search of areas of lower parasite density. Certainly physical feeding space is not limited at the densities we have observed. FORD (1986) demonstrated that continual bleeding of oysters could decrease hemolymph quality. However, as discussed earlier, there is no evidence that patches ceased to attract snails, nor did patches gradually disintegrate once formed. Hence, interference, directly as a result of decreased feeding space or indirectly by gradually reducing host acceptability as snail feeding continued, does not seem to offer a satisfactory explanation. WAAGE & DAVIES (1986) described a case in which host irritation increased at high parasite densities resulting in decreased parasite feeding efficiency. Oysters close their valves more frequently when snails feed (WARD & LANGDON, 1986), thus disrupting snail feeding. Perhaps this mechanism limits the size of snail patches by decreasing snail feeding efficiency and initiating emigration. SUTHERLAND (1983) lists a wide variety of other direct and indirect interference phenomena that might affect parasite or predator efficiency. Why *Boonea impressa* continually relocates from patch to patch remains an important question if we are to understand this snail's spatial distribution and its impact on oyster populations.

Despite the continual relocation of snails, patches retained their integrity for at least 4 to 5 days, the duration of our experiments, without any sign of dissipating. Consequently, some oysters remain parasitized by many snails for periods of time long enough to affect scope for growth, fecundity, and disease incidence (*e.g.*, WHITE *et al.*, 1984, 1987, in press). The contagious distribution of *Boonea impressa* on oysters may be responsible for the patchy distribution of *Perkinsus marinus* on many reefs, for example. Moreover, some oysters in the population will be nearly snail free. Consequently, a refuge from snail parasitism exists, but the location is not predictable. Chance plays an important role in the distribution of patches. The extent to which refugia are a permanent feature depends upon the temporal stability of patches beyond the 5 to 6 day time period we used in these experiments. Regardless of their temporal stability, patches clearly are spatially more stable than the individuals that compose them. Hence, the effect of this parasite on its host population depends more upon the temporal and spatial dynamics of the patch than on the parasites themselves.

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LITERATURE CITED

ALLEN, J. F. 1958. Feeding habits of two species of *Odostomia*. Nautilus 72:11–15.

ANDERSON, R. M. & D. M. GORDON. 1982. Processes influ-

encing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. Parasitology 85:373–398.

BULLOCK, R. C. & K. J. BOSS. 1971. Non-specificity of host-selection in the ectoparasitic snail *Odostomia* (*Menestho*) *bisuturalis* (Say) (Gastropoda: Pyramidellidae). Breviora 363: 1–17.

CATTERALL, C. P. & I. R. POINER. 1983. Age- and sex-dependent patterns of aggregation in the tropical gastropod *Strombus luhuanas*. Mar. Biol. 77:171–182.

CHANTARASA-ARD, S., Y. HIRASHIMA AND T. MIURA. 1984. Ecological studies on *Aragrus incarnatus* Haliday (Hymenoptera: Mymaridae), an egg parasitoid of the rice planthoppers I. Functional response to host density and mutual interference. Jour. Fac. Agric. Kyushu Univ. 29:59–66.

CHESSON, P. L. & W. W. MURDOCH. 1986. Aggregation of risk: relationships among host-parasitoid models. Amer. Natur. 127:696–715.

ELLIOTT, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Publ. No. 25. Ambleside (U.K.). 157 pp.

FEARE, C. J. 1971. The adaptive significance of aggregation behaviour in the dogwhelk *Nucella lapillus* (L.). Oecologia 7:117–126.

FORD, S. S. 1986. Effect of repeated hemolymph sampling on growth, mortality, hemolymph protein and parasitism of oysters, *Crassostrea virginica*. Comp. Biochem. Physiol., A, Comp. Physiol. 85:465–470.

FRETTER, V. 1951. *Turbonilla elegantissima* (Montagu), a parasitic opisthobranch. Jour. Mar. Biol. Assoc. U.K. 30:37–47.

FRETTER, V. & A. GRAHAM. 1949. The structure and mode of life of the Pyramidellidae, parasitic opisthobranchs. Jour. Mar. Biol. Assoc. U.K. 28:493–532.

GARRITY, S. D. & S. C. LEVINGS. 1984. Aggregation in a tropical neritid. Veliger 27:1–6.

GERHART, D. J. 1986. Gregariousness in the gorgonian-eating gastropod *Cyphoma gibbosum*: tests of several possible causes. Mar. Ecol. Prog. Ser. 31:255–263.

HARTNOLL, R. J. & S. J. HAWKINS. 1985. Patchiness and fluctuations on moderately exposed rocky shores. Ophelia 24:53–63.

HASSELL, M. P. 1982a. Patterns of parasitism by insect parasitoids in patchy environments. Ecol. Entomol. 7:365–377.

HASSELL, M. P. 1982b. What is searching efficiency? Ann. Appl. Biol. 101:170–175.

HAZLETT, B. A. 1984. Daily movements of some tropical marine gastropods. Mar. Behav. Physiol. 11:35–48.

HOPKINS, S. H. 1956. *Odostomia impressa* parasitizing southern oysters. Science 124:628–629.

HUFFAKER, C. B., C. E. KENNETT & T. L. TASSAN. 1986. Comparisons of parasitism and densities of *Parlatoria oleae* (1952–1982) in relation to ecological theory. Amer. Natur. 128:379–393.

MACKIN, J. G. 1962. Oyster disease caused by *Dermocystidium marinum* and other microorganisms in Louisiana. Publ. Inst. Mar. Sci. Univ. Tex. 7:132–229.

MORRISON, G. 1986. "Searching time aggregation" and density dependent parasitism in a laboratory host-parasitoid interaction. Oecologia 68:298–303.

NAGEL, M. G. & W. H. CADE. 1983. On the role of pheromones in aggregation formation in camel crickets, *Ceuthophilus secretus* (Orthoptera: Gryllacrididae). Can. Jour. Zool. 61:95–98.

OKUBO, A. 1980. Diffusion and ecological problems: mathematical models. *In:* K. Krickeberg & S. A. Levin (eds.), Biomathematics. Vol. 10. Springer-Verlag: New York. 254 pp.

POWELL, E. N., M. E. WHITE, E. A. WILSON & S. M. RAY. 1987. Small-scale spatial distribution of a pyramidellid snail ectoparasite, *Boonea impressa*, in relationship to its host, *Crassostrea virginica*, on oyster reefs. P.S.Z.N.I. Mar. Ecol. 8: 107–130.

RAY, S. 1966. A review of the culture method for detecting *Dermocystidium marinum* with suggested modifications and precautions. Proc. Natl. Shellfish. Assoc. 54:55–69.

RHODE, R. & R. SANDLAND. 1975. Factors influencing clustering in the intertidal snail *Cerithium moniliferum*. Mar. Biol. 30:203–215.

ROBERTSON, R. & V. ORR. 1961. Review of pyramidellid hosts, with notes on an *Odostomia* parasitic on a chiton. Nautilus 74:85–91.

SUTHERLAND, W. J. 1983. Aggregation and the 'ideal free' distribution. Jour. Anim. Ecol. 52:821–828.

VINSON, S. B. 1976. Host selection by insect parasitoids. Ann. Rev. Entomol. 21:109–133.

WAAGE, J. K. 1983. Aggregation in field parasitoid populations: foraging time allocation by a population of *Diadegma* (Hymenoptera, Ichneumonidae). Ecol. Entomol. 8:447–453.

WAAGE, J. K. & C. R. DAVIES. 1986. Host-mediated competition in a bloodsucking insect community. Jour. Anim. Ecol. 55:171–180.

WARD, J. E. & C. J. LANGDON. 1986. Effects of the ectoparasite *Boonea* (=*Odostomia*) *impressa* (Say) (Gastropoda: Pyramidellidae) on the growth rate, filtration rate, and valve movements of the host *Crassostrea virginica* (Gmelin). Jour. Exp. Mar. Biol. Ecol. 99:163–180.

WEIS, A. E. 1983. Patterns of parasitism by *Torymus capite* on hosts distributed in small patches. Jour. Anim. Ecol. 52: 867–877.

WHITE, M. E., E. N. POWELL & C. L. KITTING. 1984. The ectoparasitic gastropod *Boonea* (=*Odostomia*) *impressa*: population ecology and the influence of parasitism on oyster growth rates. P.S.Z.N.I. Mar. Ecol. 5:283–299.

WHITE, M. E., E. N. POWELL, S. M. RAY & E. A. WILSON. 1987. Host-to-host transmission of *Perkinsus marinus* in oyster (*Crassostrea virginica*) populations by the ectoparasitic snail *Boonea impressa*. Jour. Shellfish Res. 6:1–5.

WHITE, M. E., E. N. POWELL & S. M. RAY. In press. Effect of parasitism by the pyramidellid gastropod *Boonea impressa* on the net productivity of oysters (*Crassostrea virginica*). Estuarine Coastal Shelf Sci.

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Spawning, Egg Mass Formation, and Larval Development of the Trochid Gastropod *Margarites helicinus* (Fabricius)

by

ALAN R. HOLYOAK[1]

Department of Zoology, Brigham Young University, Provo, Utah 84602, U.S.A.

Abstract. Spawning, egg mass production, and larval development through metamorphosis and hatching of the trochid gastropod, *Margarites helicinus* were observed. Eggs were released in a mucous string which was formed into an egg mass by the foot of the spawning female and attached to a substrate via mucous threads. One or more male snails were always in attendance during egg release and egg mass formation, but release of sperm was not seen. Larvae bypassed planktonic stages and crawled from egg masses as metamorphosed snails after 12 days. Egg masses produced by *M. helicinus* from the San Juan Islands (Washington, U.S.A.) were larger and contained more eggs than those produced by populations from the United Kingdom and Greenland. The development of larvae from all populations, however, is identical.

INTRODUCTION

The reproduction of *Margarites helicinus* (Fabricius) from the Pacific coast of North America has not been studied in detail. This paper presents a description of spawning, egg mass formation, and development for *M. helicinus* collected in the San Juan Islands, Washington, U.S.A., in March and April of 1985. The egg masses and development of *M. helicinus* from the San Juan Islands are also compared with descriptions of snails from the United Kingdom (Jeffreys, 1865; Fretter, 1955) and Greenland (Thorson, 1935).

MATERIALS AND METHODS

The individuals of *Margarites helicinus* used in this study spontaneously spawned egg masses in running seawater in the laboratory and attached them to the broad-bladed brown alga *Agarum fimbriatum* (Harvey, 1862). Nine of these egg masses were selected for observation. The number of eggs per mass was counted and the size of each mass was measured. Portions of blades bearing the newly laid egg masses were cut out and isolated in beakers which were then put in running seawater (7–9°C). A pipette was used to take samples from the nine egg masses periodically so that the timing and description of the developmental stages could be recorded.

Several more egg masses not used to determine patterns of development were left untouched so that changes in physical appearance could be observed. These egg masses were then compared to masses collected in the field.

RESULTS

Spontaneous spawning was observed in the laboratory from late March through April 1985 in water that was 7–9°C. *Margarites helicinus* egg masses were also seen on *Agarum* blades in the field during the same time period.

Prior to spawning two to four snails moved close together. A female then began to release eggs in a mucous string that was 2 or 3 eggs wide. Ejaculation of sperm was not observed during egg release or egg mass formation. Eggs were formed into a mass by the female's foot. The leading edge of the foot was repeatedly extended up into the mantle cavity and then moved down toward the substrate, molding recently released eggs onto the side of the existing mass (Figure 1A). The method of attaching the egg mass to the substrate was not observed, but finished egg masses were anchored at both ends and occasionally at additional points by mucous threads (Figure 1B). Egg mass formation lasted 0.5–1.5 h. After the egg masses were completed, the snails that did not release eggs, but were

[1] Present address: Institute of Marine Science, University of California, Santa Cruz, California 95064, U.S.A.

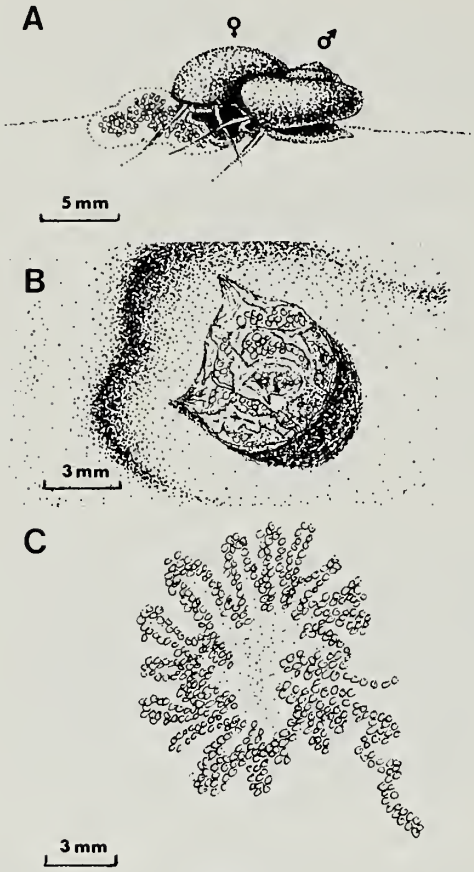

Figure 1

Egg mass production by *Margarites helicinus*. A. Male and female snails in close proximity during egg release and egg mass formation. B. A completed egg mass with mucous thread anchors attached to a depression on an *Agarum* blade. C. An egg mass compressed between a microscope slide and a cover slip.

associated with a spawning female, were sexed and found to be males.

The nine egg masses contained 95–377 eggs per mass ($\bar{x}$ = 239.2; SD = 101.3), ranged from 5–8 mm in diameter ($\bar{x}$ = 6.53 mm; SD = 1.08), and were spherical to oblong in shape. Eggs within the masses were arranged in a distinctive pattern, readily seen when a mass was pressed between a microscope slide and cover slip (Figure 1C).

Egg masses not used to follow development remained in the seawater table and soon collected particulate matter on the outer layer of mucus, obscuring many of the eggs from view. Egg masses from the field also had particulate matter covering much of their surfaces.

Eggs were 180 μm in diameter and orange to pinkish red in color. Each egg was surrounded by a 6–35 μm wide space bounded by a fertilization membrane and a transparent gelatinous coat 65–130 μm thick (Figure 2A).

Sperm were visible throughout the egg masses, between gelatinous coats of eggs, and at egg and fertilization membranes just after the egg masses were formed. Nearly 100% of the eggs in the sample were fertilized.

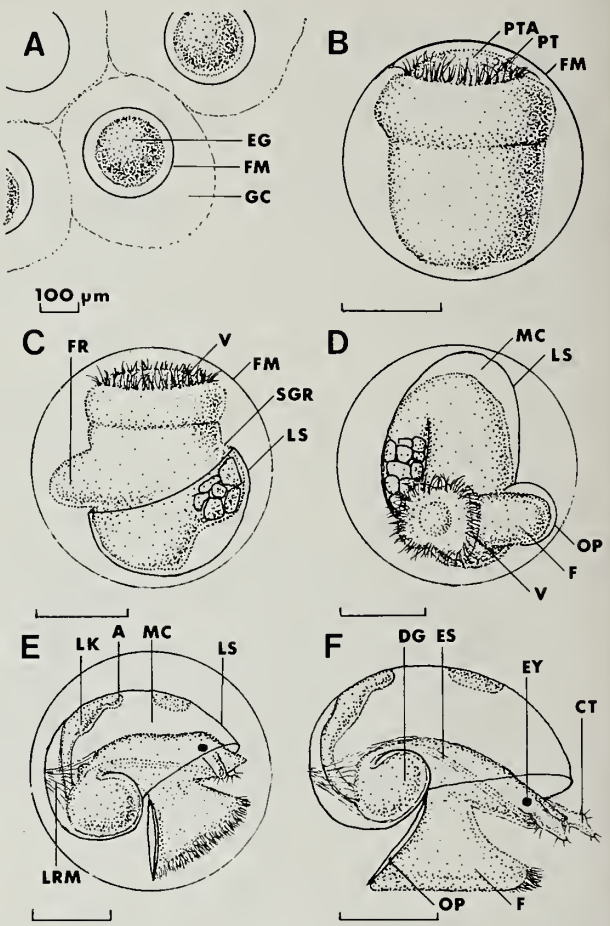

Figure 2

Developmental stages of *Margarites helicinus*. All scale bars represent 100 μm. A. Fertilized egg in an egg mass: EG, egg; FM, fertilization membrane; GC, gelatinous coat. B. Trochophore: FM, fertilization membrane; PTA, pretrochal area; PT, prototroch. C. Early veliger: FM, fertilization membrane; FR, foot rudiment; LS, larval shell; SGR, shell gland region; V, velum. D. Veliger midway through torsion: F, foot; LS, larval shell; MC, mantle cavity; OP, operculum; V, velum. E. Metamorphosed snail: A, anus; LK, larval kidney; LRM, larval retractor muscle; LS, larval shell; MC, mantle cavity. F. Hatched snail: CT, cephalic tentacle; DG, digestive gland; ES, esophagus; EY, eye; F, foot; OP, operculum.

Development proceeded in a spiral cleavage pattern. The first two cleavages were meridional, equal, and holoblastic. The third cleavage was equatorial and unequal. After two days the developing larvae became trochophores (Figure 2B). For a timetable of development see Table 1.

During the trochophore stage the foot rudiment and shell gland formed and the larval shell became visible. The prototroch then began to enlarge, forming a velum, and the larva became a veliger (Figure 2C).

During the veliger stage the foot, shell, and velum continued to develop and an operculum was formed. The velum enlarged into a bilobate structure. Within the region of the digestive gland several large (possibly yolky) cells

persisted. Veligers also underwent torsion, which took 0.5–1.5 days to complete (Figure 2D).

Prior to metamorphosis the bottom of the foot was ciliated, cephalic tentacles protruded through the velum, and eyes were visible at the base of the tentacles. During metamorphosis the velum was sloughed off and the snails were able to withdraw into their shells (Figure 2E). Two days after metamorphosis the snails crawled out of the egg masses (Figure 2F).

The entire developmental process took 12 days.

DISCUSSION

Margarites helicinus from the San Juan Islands spawns in the early spring, as was evidenced by spontaneous spawning in the laboratory in March and April and by the presence of *M. helicinus* egg masses on *Agarum* in the field during the same time period. This is 2–3 months earlier than spawning by *M. helicinus* populations in Greenland fjords, which spawn in the late summer months (THORSON, 1935).

Substrate selection for egg attachment is similar for populations in the San Juan Islands, Greenland, and the United Kingdom. Egg masses are attached to blades of algae: *Agarum* in the San Juan Islands, *Fucus* sp. and *Laminaria* sp. in Greenland (THORSON, 1935), and assorted algae in the United Kingdom (JEFFREYS, 1865; FRETTER, 1955). Snails from the United Kingdom also attach egg masses to the undersurfaces of stones (JEFFREYS, 1865; FRETTER, 1955). While the locations of egg mass deposition are quite similar, egg mass characteristics differ among the three populations.

The San Juan Islands population produces egg masses that are larger ($\bar{x}$ = 6.53 mm) and contain more eggs ($\bar{x}$ = 239) than masses produced by the other populations. The Greenland and United Kingdom populations produce masses that are 2–3 mm in diameter and hold 100–200 eggs (THORSON, 1935; FRETTER, 1955). The physical appearance of eggs also differs.

Eggs from all populations are the same size (180 μm), but eggs produced by snails from the San Juan Islands are orange to pinkish red in color, while Greenland snails produce yellowish-white eggs (THORSON, 1935). JEFFREYS (1865) reported that *Margarites helicinus* produces eggs in yellow membranous capsules, certainly an error, but did not mention egg color in his description.

Eggs within newly formed masses were surrounded by sperm. Sperm was most likely supplied by the attending male(s) as eggs were released and molded onto the egg mass. Although ejaculation of sperm was not seen, sperm were probably released very close to the egg-bearing mucous string. This would result in fertilization and explain the presence of sperm throughout the egg mass as well as aggregations of males around spawning females.

It is doubtful that sperm were transferred via spermatophore and that fertilization was accomplished within the female system before egg release for two reasons. First, one or more males were present during each spawn and left only after the egg mass was completed. Second, spermatophore transfer is known to occur in only one species of archeogastropod (FRETTER & GRAHAM, 1962).

Table 1

Timetable of the development of *Margarites helicinus*. Times are mean values for nine egg masses at 7–9°C.

Time	Stage
0.0 h	egg mass formation and fertilization
5.6 h	1st cleavage
12.5 h	2nd cleavage
18.1 h	3rd cleavage
1.3 days	gastrula
2.2 days	trochophore
2.7 days	shell formation
3.3 days	veliger
4.4–5.0 days	torsion
10.5 days	metamorphosis
12.1 days	hatching

Development in *Margarites helicinus* from the San Juan Islands is similar to that reported by THORSON (1935) and FRETTER (1955). The embryo passes the trochophore and veliger stages in the egg mass and emerges as a metamorphosed snail with a shell having 1¼ whorls and a diameter of 250 μm.

In conclusion, *Margarites helicinus* from the San Juan Islands, Washington, spawns earlier in the year and forms egg masses that are larger and contain more eggs per mass than their counterparts from Greenland and the United Kingdom. Larvae from all three locations bypass planktonic stages and emerge from egg masses as metamorphosed snails.

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LITERATURE CITED

FRETTER, V. 1955. Some observations on *Tricolia pullus* (L.) and *Margarites helicinus* (Fabricius). Proc. Malacol. Soc. Lond. 31:159–162.

FRETTER, V. & A. GRAHAM. 1962. British prosobranch molluscs. Ray Soc.: London. 755 pp.

JEFFREYS, J. G. 1865. British conchology. Vol 3. John Van Voorst: London. 393 pp.

THORSON, G. 1935. Studies on the egg-capsules and development of Arctic marine prosobranchs. Medd. om Gronland 100(5):1–71.

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Spawning and Ontogeny of *Bulla gouldiana* (Gastropoda: Opisthobranchia: Cephalaspidea)

by

BLANCA CLAUDIA FARFAN AND L. FERNANDO BÜCKLE RAMIREZ

Centro de Investigacion Cientifica y de Educacion Superior de Ensenada (C.I.C.E.S.E.), Apartado Postal 2732, Ensenada, Baja California, Mexico 22830

Abstract. In the mud flats of Baja California, spawns of *Bulla gouldiana* are found in late spring and summer. During the non-breeding season the population inhabits deeper soft-bottom zones. Regardless of the season of the year, adults kept at water temperatures equal to or greater than 24°C, and given unlimited food supply start spawning within a week. Oviposition is on average every 4 days, even in isolated specimens, although after 3–5 spawns their embryos develop gross morphological abnormalities. The number of eggs per mm of egg string ranges from 326 to 363. The number of eggs per capsule and number of capsules per mm of string are variable, but capsule size and number of eggs inside are positively correlated. Eggs and the morula, blastula, and gastrula stages are 85 μm in diameter. The late veliger measures 114 μm and is reached at 205, 137 and 114 h at 18, 24, and 28°C, respectively. Capsule size remains constant throughout embryonic development. Daily shell growth of the planktotrophic larvae is 5 μm between 18–24°C and 10 μm at 28°C. Descriptions and microphotographs of embryonic and larval development are given.

INTRODUCTION

The life history of *Bulla gouldiana* Pilsbry, 1893, is poorly known. Collective works on Pacific gastropods include short descriptions on the shell, habitat, feeding, and locomotory behavior (RICKETTS *et al.*, 1985; BRANDON & ROKOP, 1985; MCLEAN, 1978; ALLEN, 1976; ABBOTT, 1975; KEEN, 1971; MACGINITIE & MACGINITIE, 1968; JOHNSON & SNOOK, 1955). The few specific works on this opisthobranch species are related to the anatomy and functional morphology of the reproductive system (ROBLES, 1975; MARCUS, 1961), neurophysiology (BLOCK & DAVENPORT, 1982; ROBLES, 1978; ROBLES & FISHER, 1975), and the predation by *Navanax* spp. (PAINE, 1963).

LASKER *et al.* (1970) tested *Bulla gouldiana* veligers as a food source for *Engraulis mordax* larvae, but gave no description of the development of the opisthobranch. Generalities on the egg masses of this gastropod are found in several of the previously mentioned papers, but complete morphological descriptions are lacking. The present work provides descriptions of the developmental morphology of *B. gouldiana* and information on its developmental rates at different temperatures.

MATERIALS AND METHODS

Bulla gouldiana adults were collected from the intertidal mud flats of the Punta Banda Estuary, Baja California, Mexico (approximately 31°44′N, 116°38′W). They were kept in 20-L aquaria with aerated seawater at 24 ± 1°C and fed with dry pellets consisting of gluten, *Enteromorpha* sp., wheat flour (1:1:0.5) and agar as a binding agent at 10% of the primary mixture by weight.

Egg masses were removed immediately after oviposition. Their total length and volume displacement were measured. Samples were taken to estimate egg and capsule dimensions, number of embryos per capsule, and number of capsules per unit length of cord.

Incubation of the egg masses was carried out in 2-L glass beakers provided with aeration and clean seawater at three temperatures: 18, 24, and 28 ± 1°C. Spawns in which a significant number of embryos failed to show normal development or normal rotatory movements were discarded.

Culturing of the veliger larvae continued under the same temperature conditions of hatching but in 30-L polyethylene containers. The initial larval densities were set at

Table 1

Statistics of variables measured in spawns from *Bulla gouldiana* kept at 24 ± 1°C. Number of spawns analyzed (a); number of measurements (n); minimum (min); maximum (max); mean ($\bar{x}$); standard deviation (SD); interval of the mean at 95% confidence level (interval).

Variable	a	n	Min	Max	$\bar{x}$	SD	Interval
Interval between spawnings (days)	45	45	1	16	4	3	3–5
Number of eggs/mm of string	10	30	264	468	345	50	326–363
Capsule dimensions							
1–4 eggs/capsule							
Length (μm)	6	196	176	352	247	35	242–252
Width (μm)	6	196	137	286	209	25	205–212
Volume (μL)	6	196	3	16	7	3	6–7
5–12 eggs/capsule							
Length (μm)	8	256	215	462	304	42	299–309
Width (μm)	8	256	165	352	246	30	242–250
Volume (μL)	8	256	4	34	12	4	12–13
Number of capsules/mm of string							
1–4 eggs/capsule	4	12	72	117	91	14	82–100
5–12 eggs/capsule	6	18	42	76	61	10	56–66
Length of egg string in cm	36	36	29	164	78	37	66–91
Volume of egg string in mL	36	36	0.9	6	2.5	1.2	2.1–2.9

10 larvae/mL. The flagellate chrysophyte *Pavlova* (*Monochrysis*) *lutheri* (Droop) Green was provided as the food source at a concentration of 10^5 cells/mL. Food and water were replaced every 2 days.

Throughout the embryonic and larval development, samples were withdrawn at regular intervals. The progress of development was observed, measured, and photographed using a dissecting microscope.

RESULTS AND DISCUSSION

As in most opisthobranchs the eggs of *Bulla gouldiana* are encapsulated (THOMPSON, 1976). The capsules form a compact spiral string embedded in a gelatinous, layered matrix of clear mucus. The cylindrical cords can be found entwined in algae or eel grass or as free loose tangles in tidal pools of intertidal mud flats. In the collecting area, egg masses are usually found in late spring and summer. During the non-breeding season the population inhabits deeper soft-bottom zones. The length of sexually mature organisms ranges from 2 to 6 cm.

Regardless of the season of the year, adults brought into the laboratory and kept at temperatures equal to or greater than 24°C began spawning within a week. Under these conditions, food availability was apparently the limiting factor for oviposition. Ten specimens, measuring 2.4 ± 0.1 cm in shell length and weighing 4 ± 0.5 g, spawned on the average every 4 days (Table 1) when maintained over a period of 37 days at 24 ± 1°C with unlimited food supply. The slow shell growth observed in these organisms (0.21 ± 0.08 cm/month) suggests that wild specimens larger than 4 cm have experienced more than one reproductive period during their life span. This occurrence is more common in pulmonate and prosobranch gastropods than in opisthobranchs (HADFIELD & SWITZER-DUNLAP, 1984).

From a similar group of 30 adults, 36 egg masses were recovered immediately after oviposition. In different spawns the number of eggs per capsule ranged from 1 to 30; however, complete embryonic development was rarely observed in spawns with more than 12 embryos per capsule, probably owing to lack of space. In a single spawn the number of eggs per capsule was relatively constant with an estimated standard deviation of ±2.

The number of eggs per mm of string was also fairly constant. The average value of 326 ± 50 (Table 1) was estimated from 10 egg strings containing averages of 2, 4, 5, 7, and 12 embryos per capsule (two of each analyzed in three different cord positions). An analysis of variance (not presented) detected no significant differences (α = 0.05) in the number of eggs per mm of string within or among spawns, but the number of capsules per mm of string was significantly larger in egg masses with 1 to 4 embryos per capsule than in those with 5 to 12. The corresponding averages of capsules per mm of string were 91 ± 14 and 61 ± 10 (Table 1).

The sizes of the capsules were also affected by the number of embryos they contained. The two-dimensional measurements made on the capsules served as the basis for estimating capsule volume by approximation to a spheroid shape. In a regression analysis, this variable (in μL, Y) and the number of eggs inside the capsule (X) were positively correlated (r^2 = 0.65), resulting in the linear equation: $Y = 0.326 + 2.09X$. In terms of average volume, two

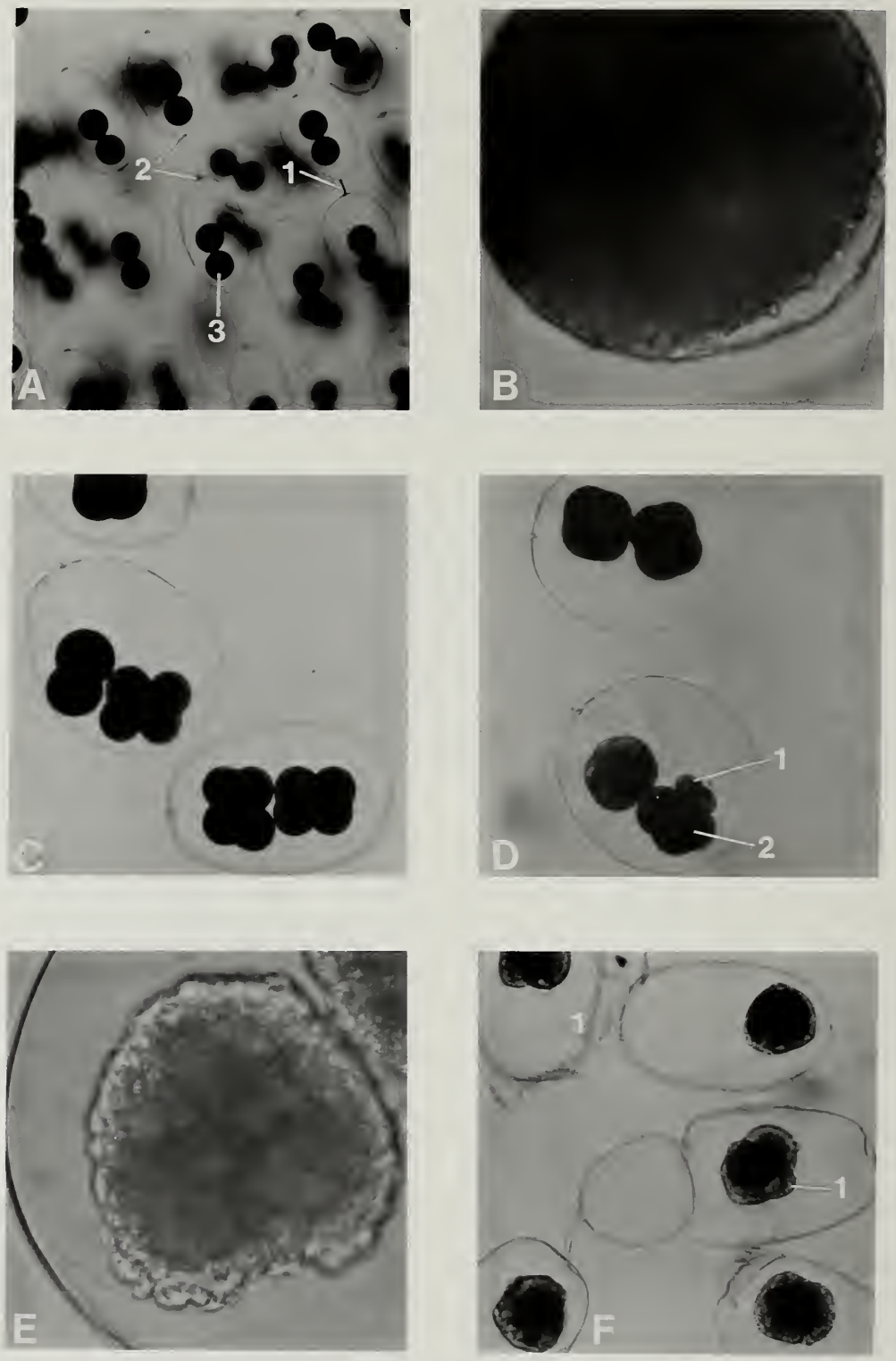

Figure 1

Embryological development of *Bulla gouldiana*. A. Gelatinous matrix with encapsulated eggs, showing chalazae (1), capsule (2), and eggs (3). B. Egg with fertilization cone. C. First and second segmentation. D. Third segmentation, showing micromeres (1) and macromeres (2). E. Early trochophore. F. Early veliger, showing velar region (1).

Table 2

Morphometry of selected embryonic stages of *Bulla gouldiana* incubated at 24 ± 1°C. Spawns analyzed (a); total number of measurements (n); minimum (min); maximum (max); mean ($\bar{x}$); standard deviation (SD); interval of the mean at 95% confidence level (interval).

	a	n	Min (μm)	Max (μm)	$\bar{x}$ (μm)	SD	Interval (μm)
Egg diameter	10	150	76	95	84.5	3.82	83.8–85.1
Diameter of blastomeres from first cleavage	6	108	54	73	63.7	5.16	62.7–64.7
Diameter of blastomeres from second cleavage	5	174	40	54	47.2	2.86	46.8–47.6
Morula	4	49	71	94	80.5	5.47	78.9–82.1
Blastula	9	123	66	99	80.3	6.55	79.2–81.5
Gastrula	9	130	66	100	85.5	6.56	84.4–86.6
Late veliger							
Maximum shell length	17	236	86	130	114.5	6.02	113.7–115.3
Maximum shell width	17	236	65	105	81.0	5.25	80.3–81.7

groups were discernible at $\alpha = 0.05$: capsules with 1 to 4 embryos, measuring 7 ± 3 μL, and those with 5 to 12 embryos, with 12 ± 4 μL in volume (Table 1).

Not all capsules were connected by chalazae, especially at the ends of the gelatinous cord (≈5 cm each side). Here the capsules were empty and the helicoidal arrangement of the string seemed to be lost. Because of the large range of cord lengths (29–164 cm, Table 1), the sequence of empty capsules was used to distinguish fragments from complete spawns. Cord length (in cm, X) and its displacement volume (in mL, Y) were well correlated ($r^2 = 0.80$). The linear equation describing this relationship was: $Y = 0.288 + 0.0295X$.

Under similar food and temperature conditions, isolated specimens of *Bulla gouldiana* and those kept in groups had comparable spawning characteristics, including oviposition frequencies. However, the embryonic development in egg masses from organisms kept in groups was mostly normal (a small number of embryos presented a compulsive, random rotation); by contrast, in the egg masses of isolated snails after three or five spawns all embryos developed gross morphological abnormalities, such as an exaggerated shell and/or body elongation, two nephrocysts, or reduced velar lobes, among others. The maximum survivorship observed in the resulting abnormal larvae was 4 days at 24°C.

The series of developmental stages of *Bulla gouldiana* described below are illustrated in Figures 1A–F and 2A–F. Dimensions are given in Table 2. When laid, the eggs (Figure 1A) measure 84.5 ± 3.8 μm. They are typical zygotes undergoing their maturation divisions. Polar bodies and a fertilization cone (Figure 1B) are readily visible. During the first and second divisions the cleavages are total and equal (Figure 1C). The resulting blastomeres measure 63.7 ± 5.2 and 47.2 ± 2.9 μm, respectively. The arrangement of micromeres at the third cleavage is characteristic of the spiral segmentation found in mollusks (Figure 1D).

The morula, blastula, and gastrula stages are similar in size to the egg (Table 2). The blastula takes the form of a stereoblastula. Apparently gastrulation is a mixture of epiboly and invagination, as found in most opisthobranchs (Thompson, 1976). A transient, elongate, bilobed gastrula (Figure 1E) develops into a trochophore, a pyriform embryo with a ciliated anterior region. In some specimens the polar bodies extruded before cleavage remain visible up to this stage.

The early veliger has two distinct regions: a bilobed velar region and a visceral hump with no visible protoconch (Figure 1F). During development, the mouth, enlarged velar lobes, a pair of statocysts underneath a ciliated foot, and a single bright red nephrocyst rapidly become evident (Figure 2B, Table 3). The undifferentiated visceral mass is covered by an incipient translucent protoconch measuring 101.0 ± 4.9 μm. In the late veliger, the stomach and digestive gland are distinct and the nephrocyst is a garnet color. The velum and operculum are fully developed. The protoconch is now 114.5 ± 6.02 μm in length. The larva constantly rotates inside the capsule by vigorous movements of the velum and appears to rasp the capsule walls. This veliger is ready to hatch (Figure 2B).

The embryonic development of *Bulla gouldiana* varies in duration as a function of temperature. Table 3 shows the chronology of selected embryonic stages observed in groups of nine egg masses, each of which was incubated at 18, 24, and 28°C. At these temperatures the mean embryonic periods were 205.5, 137.5, and 114.0 h, respectively. These values are comparable to those reported for *Acteocina canaliculata* and *Haminoea solitaria* (Franz, 1971; Harrigan & Alkon, 1978), two cephalaspideans with planktotrophic larvae and egg sizes similar to those of *B. gouldiana*.

Hatching in gastropods involves mechanical emergence, enzymatic action, or osmotic absorption of water to produce an increase in internal pressure that ruptures the egg capsule (Davis, 1981). In *Bulla gouldiana* the latter mecha-

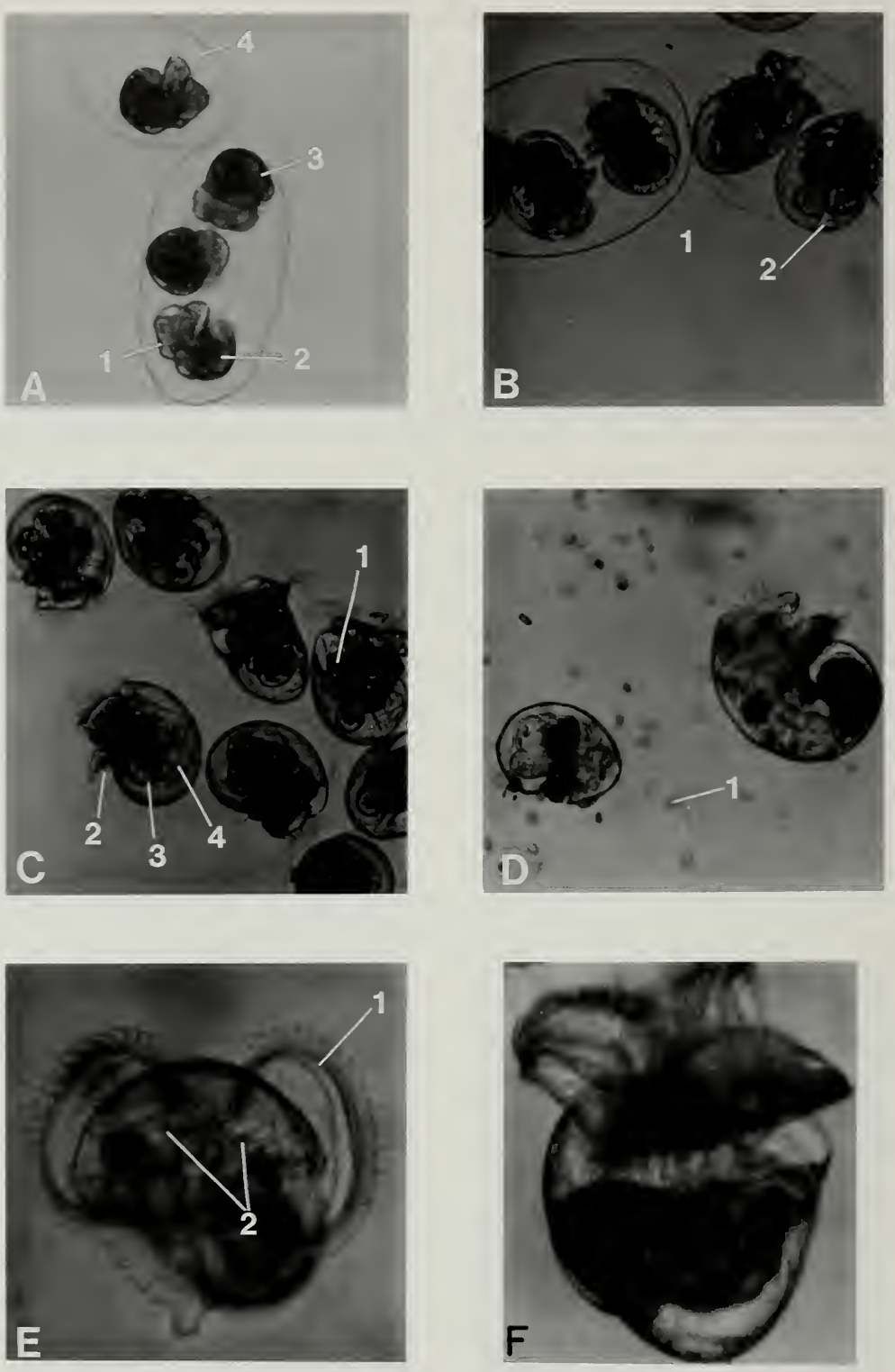

Figure 2

Embryological and larval development of *Bulla gouldiana*. A. Mid-veliger, showing velar lobes (1), nephrocyst (2), translucent protoconch (3), and foot (4). B. Late veliger in the hatching process, showing capsule (1) and retractor muscle (2). C. Hatched larvae, with garnet-color nephrocyst (1), operculum (2), digestive gland (3), and stomach (4). D. Seven-day-old veliger larva, with food particles (1). E. Ten-day-old veliger, showing velum (1) and eyes (2). F. Fifteen-day-old veliger.

Table 3

Selected embryonic stages of *Bulla gouldiana* and their development time at three temperatures. Cleavages were timed once; other values are averages from three or more observations. Time in hours.

Stage	Development time at 18°C	24°C	28°C
First cleavage	0.1	—	—
Second cleavage	3.3	—	—
Third cleavage	4.3	—	—
Morula	35.0	12.1	5.1
Gastrula	56.7	26.4	—
Trochophore	87.1	35.1	24.5
Early veliger	129.2	61.7	43.1
Mid-veliger	—	85.0	—
Late veliger	165.6	106.8	77.5
Hatching veliger	205.5	137.5	114.0

nism is probably not involved. In a test of analysis of variance (not presented) the size of the capsules at oviposition, mid-veliger, and late veliger were found not to be significantly different ($\alpha = 0.05$). Hatching probably is facilitated by the mechanical action exerted by the velum, and maybe the tip of the operculum, of the rotating veliger. The gelatinous matrix loses its flexibility and gel state and becomes easy to fragment by mechanical means (for example strong aeration) allowing an easier escape of the larvae.

The planktotrophic larva starts feeding within the first 24 h of emergence. Food particles can be observed rotating inside a zone of rodlike bodies. Below 170 μm in length there are no conspicuous changes in the general morphology of the larva except for the enlargement of the nephrocyst. Shell growth proceeds slowly, on average 5 μm/day between 18 and 24°C and 10 μm/day at 28°C.

The eyes, two black dots at the base of the velum, appear when the larva exceeds 170 μm in length (Figure 2E), and the veliger now tends to spend more time at the bottom of the culture container. Growth in shell width accelerates, resulting in a less elongate shell. In larvae larger than 230 μm, the growth of the foot separates the operculum from the shell (Figure 2F).

Despite many efforts, metamorphosis in *Bulla gouldiana* was not observed. The maximum shell length attained was 250 μm but, generally, the cultures collapsed before this larval size. Exposure of larvae to slides covered with a film of mud, phytoplankton, adult mucous trails, and combinations of these, which are metamorphic triggers for *Acteocina canaliculata* and *Haminoea vesicula* (Franz, 1971; Harrigan & Alkon, 1978), did not induce metamorphosis in *B. gouldiana*.

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LITERATURE CITED

Abbott, R. T. 1975. American sea shells. 2nd ed. Van Nostrand Reinhold Co. Ltd.: Workingham, Berks., U.K. 663 pp.

Allen, R. K. 1976. Common intertidal invertebrates of southern California. Peek Publications: Palo Alto, California. 315 pp.

Block, G. D. & P. A. Davenport. 1982. Circadian rhythmicity in *Bulla gouldiana*. Role of the eyes in controlling locomotor behavior. Jour. Exp. Zool. 224(1):57–64.

Brandon, J. L. & F. J. Rokop. 1985. Life between the tides. The natural history of common seashore life of southern California. Amer. Southwest Pub. Co.: San Diego, California. 230 pp.

Davis, C. C. 1981. Mechanisms of hatching in aquatic invertebrate eggs. Oceanogr. Mar. Biol. Ann. Rev. 19:95–123.

Franz, D. R. 1971. Development and metamorphosis of the gastropod *Acteocina canaliculata* (Say). Trans. Amer. Microsc. Soc. 90:174–182.

Hadfield, M. G. & M. Switzer-Dunlap. 1984. Opisthobranchs. Pp. 209–350. *In:* K. M. Wilbur (ed.), The Mollusca. Vol. 7, Reproduction.

Harrigan, J. F. & D. L. Alkon. 1978. Laboratory cultivation of *Haminoea solitaria* (Say, 1822) and *Elysia chlorotica* (Gould, 1870). Veliger 21(2):229–305.

Johnson, M. E. & H. J. Snook. 1955. Seashore animals of the Pacific coast. MacMillan Co.: New York, New York. 659 pp.

Keen, A. M. 1971. Sea shells of tropical west America. Marine mollusks from Baja California to Peru. Stanford University Press: Stanford, California. 1004 pp.

Lasker, R., H. M. Feder, G. H. Theilacker & R. C. May. 1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. 5(4):345–353.

MacGinitie, G. E. & N. MacGinitie. 1968. Natural history of marine animals. 2nd ed. MacGraw-Hill Book Co.: New York, New York. 523 pp.

Marcus, E. 1961. Opisthobranch mollusks from California. Veliger 3(Suppl. 1):1–85.

McLean, J. H. 1978. Marine shells of southern California. Natur. Hist. Mus. Los Angeles Co., Sci. Ser. 24. 104 pp.

Paine, R. T. 1963. Food recognition and predation on opisthobranchs by *Navanax inermis* (Gastropoda: Opisthobranchia). Veliger 6(1):1–9.

Rickets, E. F., J. Calvin & J. W. Hedgpeth. 1985. Between Pacific tides. 5th ed. Revised by D. W. Phillips. Stanford University Press: Stanford, California. 680 pp.

Robles, L. J. 1975. The anatomy and functional morphology of the reproductive system of *Bulla gouldiana* (Gastropoda Opisthobranchia). Veliger 17(3):278–291.

Robles, L. J. 1978. Accumulation and identification of lipofuscin-like pigment in the neurons of *Bulla gouldiana* (Gastropoda: Opisthobranchia). Mech. Ageing Dev. 7(1):53–64.

Robles, L. J. & S. K. Fisher. 1975. Acid phosphatase localization in neurons of *Bulla gouldiana*. (Gastropoda: Opisthobranchia). Cell. Tissue Res. 157:217–225.

Thompson, T. E. 1976. Biology of opisthobranch molluscs. Vol. 1. The Ray Society: London. 206 pp.

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The Influence of Salinity on the Distribution of Two Oregon Chiton Species (*Katharina tunicata* Wood and *Mopalia hindsii* Reeve)

by

DAVID C. ROSTAL[1] AND LEONARD SIMPSON

Portland State University, Department of Biology, Portland, Oregon 97207, U.S.A.

Abstract. Adult individuals of *Katharina tunicata* and *Mopalia hindsii* were tested for osmotic stress tolerance and oxygen consumption rates in a series of salinities (120, 100, 80, 60, and 40% seawater). *Katharina tunicata* and *M. hindsii* displayed similar trends in percent body weight variation, volume regulatory responses, and oxygen consumption rates to osmotic stress. *Katharina tunicata* exhibited a significantly greater increase in body weight than did *M. hindsii* in response to hypoosmotic conditions (80, 60, and 40% seawater). Both species showed reduced oxygen consumption rates and significantly increased weight gain in 40% seawater. Salinity was measured twice monthly at two study sites. Salinity measurements revealed a difference in mean salinity between study sites of 12% seawater. Variation in dominant macroalgal species between study sites reflected published dietary characteristics: *K. tunicata* feeds on *Hedophyllum sessile,* while *M. hindsii* feeds on *Gigartina* spp. and animal material. Salinity appears not to influence the distribution of adult *K. tunicata* and *M. hindsii.* The results of this study suggest that both species are osmoconformers with equivalent volume regulatory capabilities and are weakly euryhaline. Other factors such as diet, larval settling responses, and interspecific competition may be involved in the difference observed in the distribution of *K. tunicata* and *M. hindsii.*

INTRODUCTION

The effect of salinity on the physiology and ecology of marine mollusks is receiving increased attention. PROSSER (1973) stated that marine mollusks are osmoconformers with various degrees of stenohalinity. More recent evidence suggests that many marine mollusks—*e.g., Littorina neritoides* Linnaeus, *Collisella digitalis* (Rathke, 1833), *Tectura scutum* (Rathke, 1833), *Modiolus* spp., and *Mopalia muscosa* (Gould, 1846)—possess mechanisms for active volume regulation and are euryhaline (BURTON, 1983).

The physiology of several chiton species has been investigated. BOYLE (1969) studied the survival of *Sypharochiton pelliserpentis* (Quoy & Gaimard, 1835) exposed to osmotic stress conditions and concluded that this species could osmoconform to salinities ranging from 50 to 150% seawater. *Cyanoplax hartwegii* (Carpenter, 1855) can osmoconform over a salinity range of 75 to 125% seawater and is capable of volume regulation (MCGILL, 1976). Environmental acclimation to varying salinity was observed to influence osmotic stress tolerances between two populations of *Nuttallina californica* (Reeve, 1847) (SIMONSEN, 1976). The osmotic concentration of hemolymph in *Katharina tunicata* (Wood, 1815) fluctuated with tidal fluctuation in osmotic concentration but did not vary during exposure to air (STICKLE & DENOUX, 1976). STICKLE & AHOKAS (1975) postulated that *Mopalia muscosa* is less susceptible to osmotic stress than *K. tunicata.* Variations in temperature and salinity from normal seawater also influence oxygen consumption in *Mopalia lignosa* (Gould, 1846) (LEBSACK, 1976).

Chitons occur along rocky shores in the intertidal and subtidal zones in all seas and latitudes (HYMAN, 1967). ANDRUS & LEGARD (1976) compared the habitats of 12 chiton species along the California coast and concluded that surf strength, light exposure, substrate composition, moisture, and biological associates were all important in determining habitat selection. PIERCY (1987) observed differences in the diet and microhabitat of six eastern Pacific chiton species and suggested that mechanisms such as resource partitioning or "indirect commensalism" may help maintain chiton diversity.

[1] Address reprint requests to David C. Rostal, Department of Biology, Texas A&M University, College Station, Texas 77843.

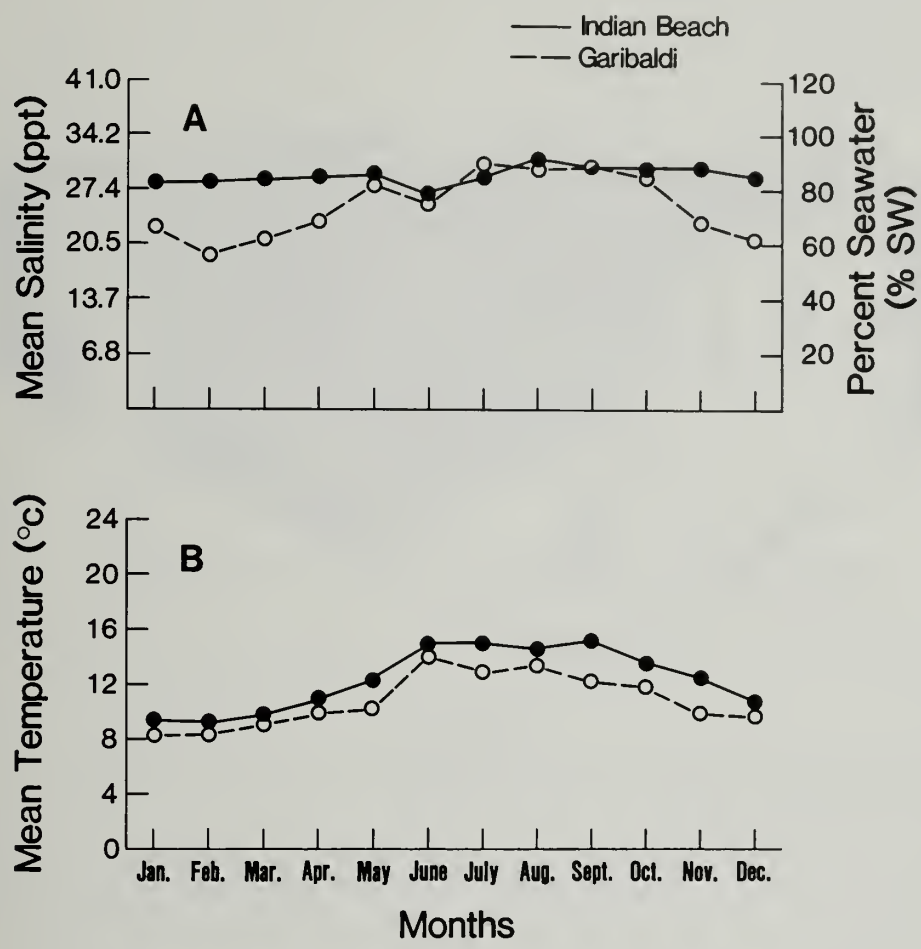

Figure 1

Mean monthly salinity (A, ppt) and mean monthly water temperature (B, °C) for Indian Beach and Garibaldi study sites. Maximum measured salinity and temperature variation was ±5.76 ppt and 2.94°C for Indian Beach (*n* averaged 62 measurements per month) and ± 14.69 ppt and 5.70°C for Garibaldi site (*n* averaged 15 measurements per month).

In this study, the influence of salinity on distribution was investigated in two sympatric chiton species, *Katharina tunicata* (Wood, 1815) and *Mopalia hindsii* (Reeve, 1847). *Katharina tunicata* is generally restricted to open coast habitats and is considered stenohaline, while *M. hindsii* is common to open ocean as well as slightly brackish habitats and is considered euryhaline. The objectives of this research were to compare the osmotic stress tolerance, volume regulatory capabilities, and influence of salinity on oxygen consumption rates in these two species. These results will be discussed with regard to variation in distribution and ecology.

MATERIALS AND METHODS

Study Sites

An open coast and a brackish water study site were chosen for *Katharina tunicata* (Indian Beach, Ecola State Park, Oregon) and *Mopalia hindsii* (Garibaldi, Tillamook Bay, Oregon) respectively. Site selection was based on salinity and temperature characteristics as well as intertidal indicator species.

Indian Beach, Ecola State Park, Clatsop County, Oregon (45°55′N) has a large rock and boulder outcrop at the south end of the beach where wave action is strong. *Katharina tunicata* is common in this location with *Mopalia hindsii* and *Tonicella lineata* (Wood, 1815) also present. Other common open coast organisms present are *Pisaster ochraceus* (Brandt, 1835), *Mytilus californianus* Conrad, 1837, *Hemigrapsus nudus* (Dana, 1851), and *Pollicipes polymerus* (Sowerby, 1833). Mean annual salinity is 29.06 ppt (85% seawater) and mean annual temperature is 12.4°C (Figure 1, Seaside Aquarium Data; Bourke & Glenne, 1971).

Garibaldi, Tillamook Bay, Tillamook County, Oregon (45°34′N) has a shale outcrop with small to large loose

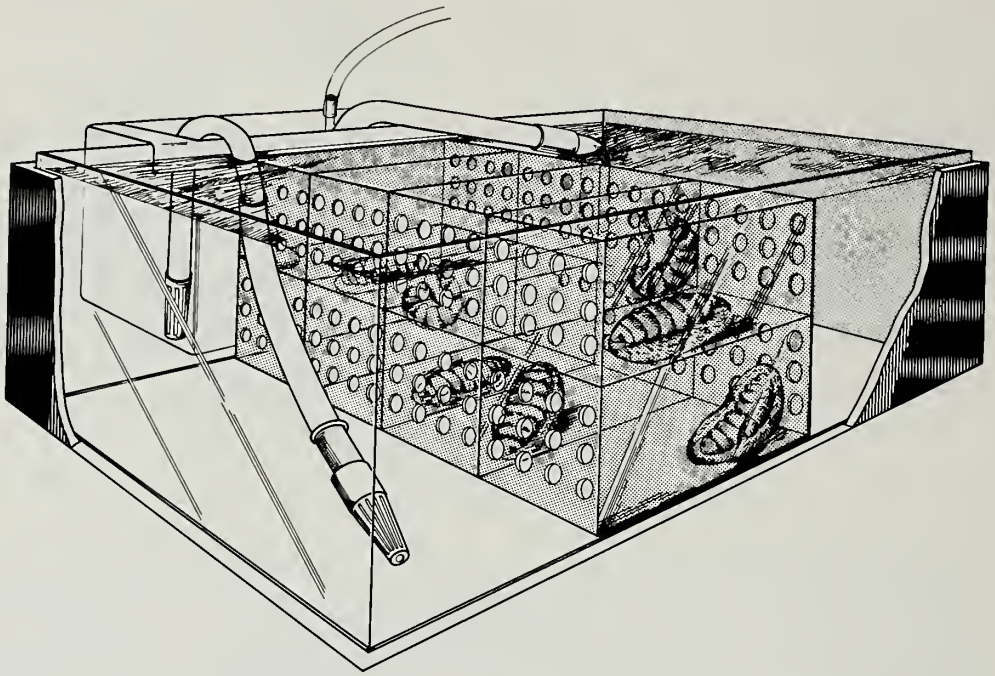

Figure 2

Osmotic stress test apparatus used to measure osmotic stress tolerance and volume regulatory rates of adult *Katharina tunicata* and *Mopalia hindsii*. Specimens (8 per test) were held in individual chambers that allowed free movement and continuous circulation of seawater.

rocks at the north end of the bay and weak wave action. *Mopalia hindsii* and *Mopalia muscosa* are found under the rocks and in crevices during low tide. Other common brackish water organisms present are *Hemigrapsus oregonensis* (Dana, 1851), *Mytilus edulis* Linnaeus, 1758, *Pagurus* spp., and *Thais emarginata* (Deshayes, 1839). Mean annual salinity is 25.47 ppt (75% seawater) and mean annual temperature is 10.9°C (Figure 1, data from the State of Oregon, Department of Environmental Quality, Portland, Oregon).

Osmotic Stress Tests

Adults of *Katharina tunicata* (mean weight = 10.23 g) and *Mopalia hindsii* (mean weight = 10.90 g) were collected at study sites and acclimated in 34 ppt synthetic seawater (100% SW, Instant Ocean Synthetic Sea Salts, Aquarium Systems, Inc.) at 11°C and 16L:8D photoperiod for two weeks prior to testing. Eight animals of each species were exposed to a test salinity (120, 100, 80, 60, and 40% SW) for 36 h in an osmotic test apparatus (Figure 2). Animals were fully submerged in individual chambers which allowed free movement and continuous circulation of seawater. Test salinities were based on the natural range observed at the study sites. At time intervals of 0, 1, 2, 4, 6, 8, 12, 24, and 36 h, animals were removed from the chambers, blotted dry with absorbent towels, and then weighed using a Mettler PC 2200 scale to the nearest 0.01 g. Animals were allowed 5 min to re-adhere in the chambers before being resubmerged in the test salinity. Percent body weight changes due to osmotic stress gradient and volume regulation were calculated.

Oxygen Consumption Tests

Oxygen consumption rates of each species were measured using a modified Scholander respirometer (Scholander, 1950). Four animals of each species were monitored in each test salinity (120, 100, 80, 60, and 40% SW) for 3–4 h at 11°C and 16L:8D photoperiod following 48 h of acclimation to the test salinity (normally post-osmotic stress testing). Oxygen consumption rates (μL/g/h) were calculated for each species per salinity.

Habitat Characteristics

Seawater samples were collected twice monthly at the two study sites during low tide from January to June 1985. Salinity (ppt) of seawater samples was determined using a YSI-33 Salinity-Conductivity-Temperature (S-C-T) Meter.

Dominant macroalgal species were collected from each study site and identified (Smith, 1969; Guberlet, 1956). Macroalgal species present at study sites were compared with published diets of the chitons (Steneck & Watling, 1982; Haderlie & Abbott, 1980).

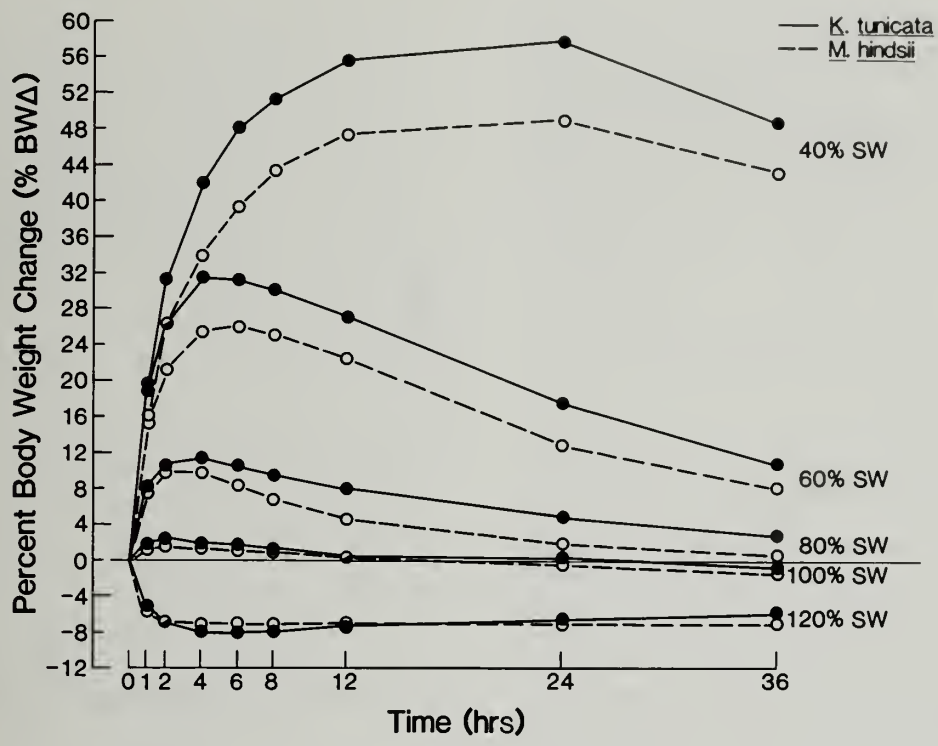

Figure 3

Mean percent body weight change and volume regulatory rates of adult specimens of *Katharina tunicata* and *Mopalia hindsii* in various test salinities over a 36-h test period at 11°C and 16L:8D photoperiod. SE was always less than 1.86% for *K. tunicata* and 2.84% for *M. hindsii*; $n = 8$ per salinity per species.

Statistical Analysis

Significant differences in osmotic stress response between *Katharina tunicata* and *Mopalia hindsii* were analyzed using a multifactor analysis of variance (repeated measures, $P < 0.05$; Winer, 1971).

Significant differences in oxygen consumption rates between *Katharina tunicata* and *Mopalia hindsii* were determined using an independent *t*-test ($P < 0.05$; Bruning & Kintz, 1977). Significant differences in oxygen consumption rates between salinities within each species were analyzed using an analysis of variance (completely randomized design, $P < 0.05$; Bruning & Kintz, 1977).

RESULTS

Osmotic Stress Tests

Adults of *Katharina tunicata* and *Mopalia hindsii* displayed similar trends in percent body weight (% BW) variation and volume regulatory responses to osmotic stress (Figure 3). *Katharina tunicata,* however, exhibited a significantly higher percent body weight increase than did *M. hindsii* in response to hypoosmotic conditions (80% SW, d.f. = 1,14, $F = 6.13$, $P < 0.05$; 60% SW, d.f. = 1,14, $F = 16.85$, $P < 0.005$; 40% SW, d.f. = 1,14, $F = 17.89$, $P < 0.001$). Following maximum percent body weight variation, both *K. tunicata* and *M. hindsii* displayed similar volume regulatory rates. Maximum percent body weight variation was measured within 4 h of exposure to 120, 100, 80, and 60% seawater (Table 1). Maximum percent body weight variation in 40% seawater, however, was not reached until 24 h following exposure (*K. tunicata* = 57.91 ± 1.57% BW, $n = 8$; *M. hindsii* = 49.32 ± 1.86% BW, $n = 8$). Both species appeared to display reduced activity and adherence capabilities in 40% seawater compared with other salinities tested.

Table 1

Maximum percent weight change for two Oregon chiton species (*Katharina tunicata* and *Mopalia hindsii*) in various salinities. Results are mean values ± SE (n).

% SW	*K. tunicata*	*M. hindsii*
120	−7.899 ± 0.181 (8)	−7.165 ± 0.248 (8)
100	2.276 ± 0.156 (8)	1.835 ± 0.325 (8)
80	11.456 ± 0.402 (8)	10.000 ± 0.527 (8)
60	31.423 ± 0.739 (8)	26.115 ± 0.907 (8)
40	57.906 ± 1.573 (8)	49.321 ± 1.864 (8)

Table 2

Oxygen consumption rates (μL/g/h) for two Oregon chiton species (*Katharina tunicata* and *Mopalia hindsii*) in various salinities. Results are mean values ± SE (n).

% SW	*K. tunicata*	*M. hindsii*
120	11.9 ± 2.2 (4)	10.6 ± 2.3 (4)
100	13.5 ± 1.3 (4)	12.7 ± 1.2 (3)
80	11.3 ± 0.6 (4)	11.7 ± 2.9 (4)
60	10.6 ± 1.7 (4)	12.4 ± 2.7 (4)
40	5.7 ± 0.9 (3)	7.6 ± 1.0 (4)

Oxygen Consumption Tests

Oxygen consumption rates in each salinity were not significantly different between *Katharina tunicata* and *Mopalia hindsii* (Table 2). *Katharina tunicata* and *M. hindsii* displayed similar trends in response to various salinities (Figure 4). The mean rate of oxygen consumption by *K. tunicata* decreased significantly with the decrease in salinity to 40% seawater (d.f. = 4,14, $F = 3.24$, $P < 0.05$). The mean rate of oxygen consumption by *M. hindsii* also decreased similarly in response to a decrease in salinity to 40% seawater; however, this decrease was not statistically significant. The reductions in mean rates of oxygen consumption in 40% seawater by both *K. tunicata* and *M. hindsii* reflect the trend observed in body weight variation and decrease in activity observed during the osmotic stress tests.

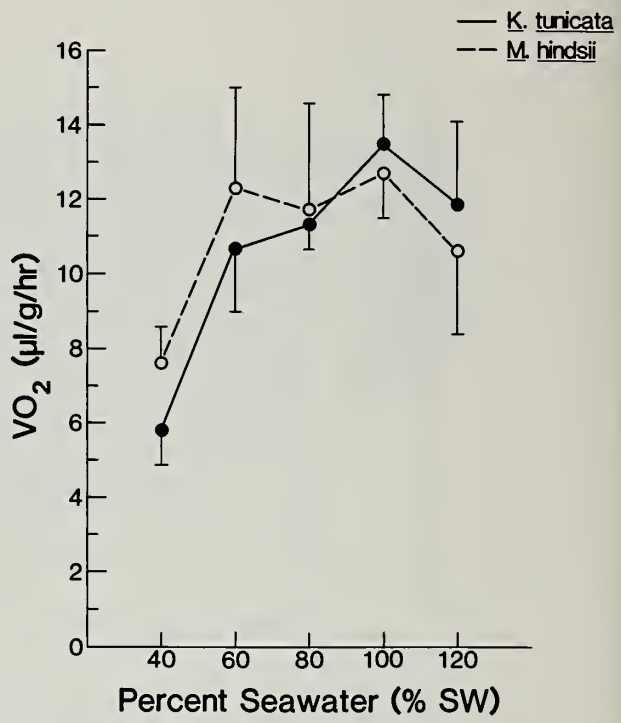

Figure 4

Mean oxygen consumption rates (VO_2) of adult specimens of *Katharina tunicata* and *Mopalia hindsii* in various test salinities at 11°C and 16L:8D photoperiod. Results are mean values ± SE.

Table 3

Dominant macroalgal species of Indian Beach, Ecola State Park and Garibaldi, Tillamook Bay study sites. ** indicates presence.

Macroalgal species	Indian Beach	Garibaldi
Rhodophyta		
Crustose coralline alga	**	
Bossiella orbigniana (Dec.) Silva, 1957	**	
Gigartina exasperata Harvey & Bailey, 1851		**
Gigartina volans (C. Ag.) J. Agardh, 1846		**
Gracilaria verrucosa (Huds.) Papenfuss, 1950		**
Gymnogongrus linearis (C. Ag.) J. Agardh, 1851	**	
Iridaea cordata (Turn.) Bory, 1826	**	**
Plocamium oregonum Doty, 1947	**	
Prionitis lanceolata (Harv.) Harvey, 1853	**	
Prionitis linearis Kylin, 1941	**	
Phaeophyta		
Fucus distichus Linnaeus, 1767	**	**
Halosaccion glandiforme (Gmel.) Ruprecht, 1851		**
Hedophyllum sessile (C. Ag.) Setchell, 1901	**	
Laminaria dentigera Kjellman, 1889	**	**
Chlorophyta		
Ulva taeniata (Setch.) Setchell & Gardner, 1920		**

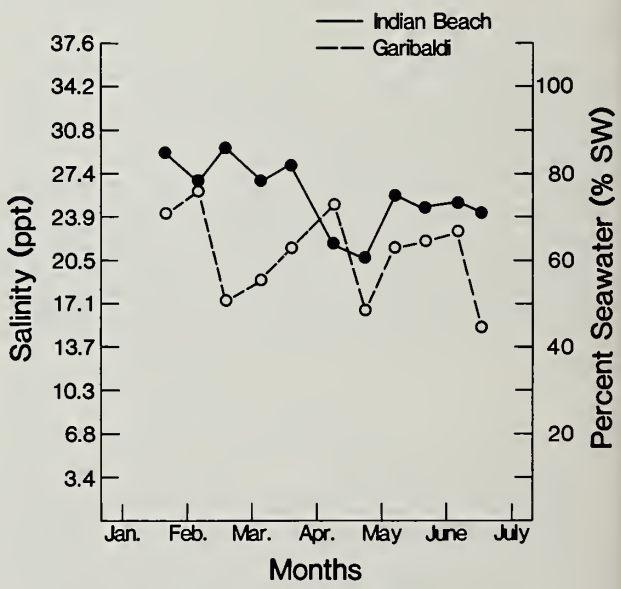

Figure 5

Twice-monthly salinity measurements collected during low tide ($n = 1$) from January to June 1985 for the Indian Beach and Garibaldi study sites.

Habitat Characteristics

Salinity measurements at low tide from January to June 1985 yielded a mean salinity of 25.63 ± 0.85 ppt, $n = 12$ (75% seawater) for the Indian Beach study site and a mean salinity of 21.04 ± 1.05 ppt, $n = 12$ (63% seawater) for the Garibaldi study site. Although mean salinities recorded during the study were lower than the mean annual salinities for the study sites (Indian Beach, 29.06 ppt; Garibaldi, 25.47 ppt), the variation in mean salinities between study sites during the study (4.59 ppt, 12% seawater) parallels the variation in mean annual salinities (3.59 ppt, 10% seawater). Measurements were taken at low tide during winter and spring months when freshwater runoff from coastal land is greatest.

Identification of dominant macroalgal species revealed variation between the Indian Beach site (six Rhodophyta, three Phaeophyta) and the Garibaldi site (four Rhodophyta, three Phaeophyta, and one Chlorophyta) in the species present (Table 3). *Hedophyllum sessile,* common in the diet of *Katharina tunicata* (STENECK & WATLING, 1982), was identified at the Indian Beach site only. *Gigartina* spp., common at the Garibaldi site, as well as animal material are reported as common in the diet of *Mopalia hindsii* (STENECK & WATLING, 1982; HADERLIE & ABBOTT, 1980).

DISCUSSION

The influence of salinity on the distribution of *Katharina tunicata* and *Mopalia hindsii* appears to be minimal. Although *K. tunicata* displayed significantly higher variation in percent body weight than did *M. hindsii* in response to hypotonic stress conditions (80, 60, and 40% SW), both species displayed similar rates of weight gain and volume regulation in all salinities tested. Both species, however, exhibited markedly increased weight gain in response to 40% seawater compared with other salinities tested. The percent weight changes observed for both *K. tunicata* and *M. hindsii* in 60–120% seawater are similar to those reported for *Cyanoplax hartwegii* in 75–125% seawater (MCGILL, 1976). BOYLE (1969) tested the osmotic stress tolerance of *Sypharochiton pelliserpentis* in 0–150% seawater and found the species tolerant of salinities ranging from 50 to 150% seawater. The response of *S. pelliserpentis* to 50% seawater, however, was similar to that observed for *K. tunicata* and *M. hindsii* in 40% seawater. The results support the hypothesis that *K. tunicata* and *M. hindsii* are osmoconformers with volume regulatory capacities and that they are similar in osmotic stress tolerance to *S. pelliserpentis, C. hartwegii,* and *Nuttallina californica* (BOYLE, 1969; MCGILL, 1976; SIMONSEN, 1976). The volume regulation observed is probably a "passive" mechanism rather than "active" since the size of the specimen appears to influence the rate of regulation (*i.e.,* larger specimens display slower rates of volume regulation).

LEBSACK (1976) reported that deviation in salinity from that of normal seawater results in a decrease in oxygen consumption rate by *Mopalia lignosa,* although the salinities LEBSACK (1976) tested ranged only from 90 to 120% seawater. Oxygen consumption rates for *Katharina tunicata* were observed to decrease significantly in response to salinity variation from 100% seawater, while oxygen consumption rates of *M. hindsii* did not. Both *K. tunicata* and *M. hindsii* displayed equally reduced mean oxygen consumption rates in response to 40% seawater. This reduction in oxygen consumption in 40% seawater paralleled the increased weight gain observed in the osmotic stress tolerance results.

The variation in mean salinity (4.59 ppt, 12% SW) during low tide observed between the Indian Beach and Garibaldi study sites from January to June 1985 is within the physiological tolerances of both *Katharina tunicata* and *Mopalia hindsii.* The increase in body weights and decrease in oxygen consumption rates of *K. tunicata* and *M. hindsii* in 40% seawater dilution, and their reduced adherence capabilities, suggest that this salinity is near or below the ecological tolerances of both species even though it is physiologically tolerable under laboratory conditions. Salinities below 40% seawater were not measured at either study site. Although *K. tunicata* is capable of tolerating 40% seawater for a limited time, the data suggest that *M. hindsii* may be more tolerant of this extreme dilution. BOYLE (1969) reported that *Sypharochiton pelliserpentis* could survive dilutions of up to 50% seawater for at least 24 h. SIMONSEN (1976) suggested that long term acclimation to variation in salinity may influence osmotic stress tolerance in *Nuttallina californica.* Thus, acclimation may account in part for the observed variation in osmotic tolerance to extreme dilution (40% SW) between *K. tunicata* and *M. hindsii.*

The diets of *Katharina tunicata* and *Mopalia hindsii* may influence the difference observed in distribution. *Hedophyllum sessile,* common in the diet of *K. tunicata,* is restricted to open coast habitats such as the Indian Beach site (HIMMELMAN, 1978; STENECK & WATLING, 1982). Common components of the diet of *M. hindsii,* several *Gigartina* spp. plus animal material, are less restricted and are common at the Garibaldi site (HADERLIE & ABBOTT, 1980; STENECK & WATLING, 1982). Further research on diets of chitons as well as the influence of herbivory on macroalgal species under controlled conditions is needed.

BOYLE (1969) suggested that microhabitat osmotic fluctuations are unlikely to limit the distribution of *Sypharochiton pelliserpentis* owing to its euryhaline characteristics. The data support a similar conclusion for *Katharina tunicata* and *Mopalia hindsii* in that both are euryhaline and display similar physiological capabilities.

Although the influence of salinity on the distribution of adult *Katharina tunicata* and *Mopalia hindsii* appears to be minimal, salinity may indirectly influence distributions in two ways: (1) the tolerance to osmotic stress of larval stages may vary significantly; and (2) the influence of salinity on macroalgal species may affect the settling responses of chiton larval stages. For example, *Tonicella lineata* larvae display a selective settling response to the crustose coralline

algae *Lithothamnium* spp. and *Lithophyllum* spp. (BARNES & GONOR, 1973).

In conclusion, our results suggest that *Katharina tunicata* and *Mopalia hindsii* are osmoconformers with equivalent volume regulatory capabilities and that they are weakly euryhaline. Other factors such as diet, larval settling responses, and interspecific competition may influence the differences observed in the distribution of *K. tunicata* and *M. hindsii* along the Oregon coast.

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LITERATURE CITED

ANDRUS, J. K. & W. B. LEGARD. 1976. Description of habitats of several intertidal chitons found along the Monterey Peninsula of central California. Veliger 18(Suppl.):3–8.

BARNES, J. R. & J. J. GONOR. 1973. The larval settling response of the lined chiton *Tonicella lineata*. Mar. Biol. 20: 259–264.

BOURKE, R. H. & B. GLENNE. 1971. The nearshore physical oceanographic environment of the Pacific Northwest coast. Reference 71-45, Department of Oceanography, Oregon State University, Corvallis, Oregon.

BOYLE, P. R. 1969. The survival of osmotic stress by *Sypharochiton pelliserpentis* (Mollusca: Polyplacophora). Biol. Bull. 136:154–166.

BRUNING, J. L. & B. L. KINTZ. 1977. Computational handbook of statistics. Scott, Foresman and Co.: Glenview, Illinois.

BURTON, R F. 1983. Ionic regulation and water balance. *In:* A. S. M. Saleuddin & R. M. Wilbur (eds.), The Mollusca. Vol. 5. Physiology 2. Academic Press: New York.

GUBERLET, M. L. 1956. Seaweeds at ebb tide. University of Washington Press: Seattle.

HADERLIE, E. C. & D. P. ABBOTT. 1980. Polyplacophora: the chitons. Pp. 412–428. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford University Press: Stanford, California.

HIMMELMAN, J. H. 1978. The reproductive cycle of *Katharina tunicata* Wood and its controlling factors. Jour. Exp. Mar. Biol. Ecol. 31:27–41.

HYMAN, L. H. 1967. The invertebrates. Vol. VI. Mollusca I. McGraw-Hill Book Co.: New York.

LEBSACK, C. S. 1976. Effect of temperature and salinity on the oxygen consumption of the chiton *Mopalia lignosa*. Veliger 18(Suppl.):94–97.

MCGILL, V. L. 1976. Response to osmotic stress in the chiton *Cyanoplax hartwegii*. Veliger 18(Suppl.):109–112.

PIERCY, R. D. 1987. Habitat and food preferences in six eastern Pacific chiton species (Mollusca: Polyplacophora). Veliger 29:388–393.

PROSSER, C. L. 1973. Comparative animal physiology. W. B. Saunders Co.: Philadelphia.

SCHOLANDER, P. F. 1950. Volumetric plastic respirometer. Review Sci. Instru. 21:378–380.

SIMONSEN, M. 1976. Response to osmotic stress in vertically separated populations of an intertidal chiton, *Nuttallina californica*. Veliger 18(Suppl.):113–116.

SMITH, G. M. 1969. Marine algae of the Monterey Peninsula. 2nd ed. Stanford University Press: Stanford, California.

STENECK, R. S. & L. WATLING. 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional approach. Mar. Biol. 68:299–319.

STICKLE, W. B. & R. AHOKAS. 1975. The effects of tidal fluctuation of salinity on the hemolymph composition of several molluscs. Comp. Biochem. Physiol. 50A:291–296.

STICKLE, W. B. & G. J. DENOUX. 1976. Effects of *in situ* tidal salinity fluctuations on osmotic and ionic composition of body fluid in southeastern Alaska rocky intertidal fauna. Mar. Biol. 37:125–135.

WINER, B. J. 1971. Statistical principles in experimental design. McGraw-Hill Book Co.: New York.

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A New Species of *Mexichromis* (Nudibranchia: Chromodorididae) from the Eastern Pacific

by

TERRENCE M. GOSLINER AND HANS BERTSCH

California Academy of Sciences, Golden Gate Park,
San Francisco, California 94118, U.S.A.

Abstract. *Mexichromis* ***amalguae*** sp. nov. is described from Isla Cedros and Islas San Benito off the Pacific coast of Baja California, Mexico. Its anatomy is contrasted with known species of *Mexichromis* and with other chromodorids that exhibit similar color patterns.

INTRODUCTION

Based on a photograph, the animal described here was first reported from Isla Cedros as an unnamed species of chromodorid (Behrens, 1980). On a recent expedition to the islands west of the Baja California peninsula, two specimens of this animal were collected. This species represents the fourth known species of *Mexichromis* in the eastern Pacific. Its anatomy is described and contrasted with its congeners. Three similarly colored chromodorids in the Mediterranean are also distinguished from our new species.

CHROMODORIDIDAE

Mexichromis Bertsch, 1977

Mexichromis ***amalguae*** Gosliner & Bertsch, sp. nov.

(Figures 1–4)

Chromodorid sp.: BEHRENS, 1980:100–101, species 140 (color photograph). *Chromodoris* sp.: HAMANN, 1984 (color photograph).

Material examined: (1) Holotype, California Academy of Sciences, CASIZ 064815; collected subtidally from 13 m depth, NE side of Isla Cedros (28°10′N, 115°15′W), 19 August 1987, by Paul Solonski.

(2) Paratype, CASIZ 064816; collected subtidally, 13 m depth, W side Isla San Benito Oeste (28°05′N, 115°30′W), 17 August 1987, by Bruce Heyer.

Etymology: When Isla Cedros was "discovered" by the Spaniard Francisco de Ulloa in 1540, the island was inhabited by a tribe of Cochimi who called the island Amalgua, or Isle of Fogs (WHEELOCK & GULICK, 1975; transliteration of the word may vary). The European conquerors misnamed the island by misidentifying its flora, and in 1732 removed the entire native American population to the Baja California mission of San Ignacio, where their culture and population were essentially eliminated by the end of the century through the "civilizing" effects of Europeanization and disease. We wish to honor a native culture and people by naming this new species based on the original name of the island. (The genus *Mexichromis* is masculine in gender; ***amalguae*** is genitive, meaning "of the isle of fogs," or "belonging to Amalgua.")

Description: External morphology: Total length of the living animal is about 20 mm. A cryptobranch dorid, this animal has an elongate, oval body shape. The dorsum is slightly humped and the surface smooth; the foot may protrude posteriorly past notal margin. The body coloration is blue to a light purple blue; a median longitudinal, cream white, diffuse dorsal stripe may be present (Figure 1B); some specimens (BEHRENS, 1980; HAMANN, 1984) lack this stripe entirely, whereas it was only faintly visible in the holotype (Figure 1A). This stripe begins medially behind the rhinophores and ends anterior to the gills. There is a thin yellow band encircling the entire notal margin. This band can vary from a bright yellow to a faint cream yellow color, although within a single individual its color does not vary. The rhinophores have 11–14 lamellae and are a deep navy blue color; the 7–9 unipinnate gills are also navy blue in color. The dark coloration of the rhinophores and gills is present in animals with lighter and darker colored dorsal surfaces. A whitish longitudinal stripe may be present on the posteriorly protruding upper surface

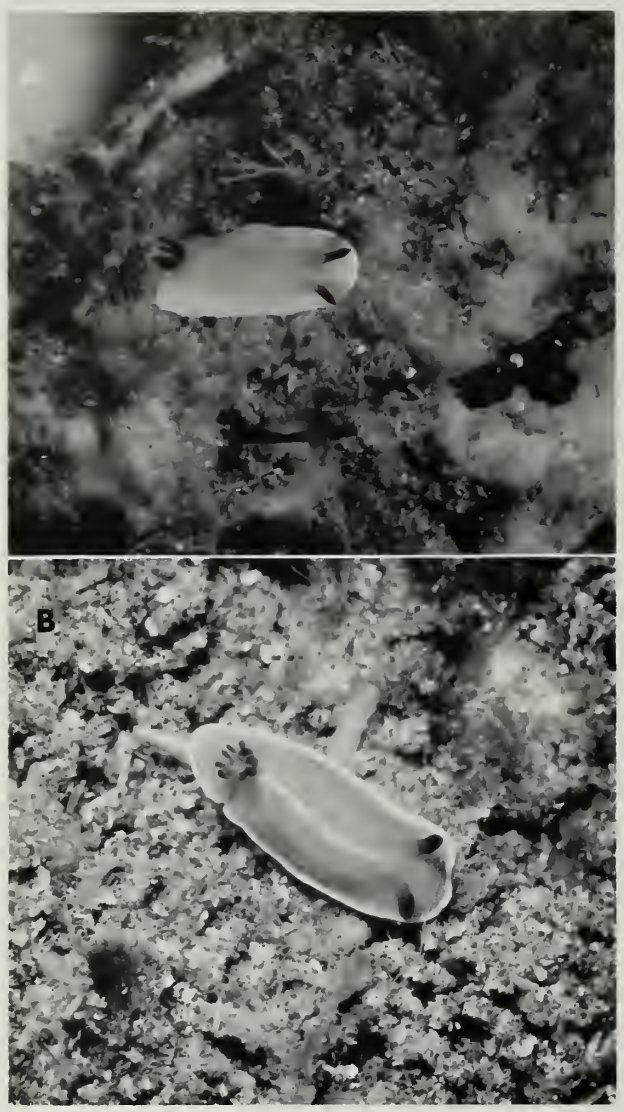

Figure 1

Mexichromis ***amalguae*** Gosliner & Bertsch, sp. nov. Dorsal views of living animals; photographs by T. M. Gosliner. A. Holotype, NE Isla Cedros. B. Paratype, Isla San Benito Oeste.

of the foot. The blue foot does not have a yellowish marginal rim.

Buccal armature: The jaws consist of numerous chitinous elements, each bearing 2 or 3 denticles (Figure 2A).

Radula: The holotype had a radular formula of 24 × 22·1·22; the paratype was 46 × 27·1·27. Both specimens had a small, thin, very low elongate rachidian. The first lateral tooth (Figures 2B–D) had 1–3 inner denticles and 3 or 4 outer denticles on each side of the central cusp. Succeeding laterals had deeply indented denticles on the posterior side of the cusp. The innermost lateral teeth appeared nearly bicuspid because of the deep cleft between the cusp and the first denticle; the length of the lower denticles was about ⅓ the total width of cusp (along the anterior-posterior axis, measuring from the front of the cusp to the tip of the denticle). The primary cusp of the middle (Figures 3A, B) and outer (Figures 3C, D) laterals shortens, so that succeeding denticles are longer. This is the strikingly "acuspidate" or "pectinate" condition described by Bertsch (1977) and Rudman (1984) for the genus *Mexichromis*. There are 4–7 prominent denticles on the posterior surface of the laterals (Figures 3A–D). The outermost laterals become shorter and have a wider anterior-posterior axis to the cusp, nearly losing the distinct basal flange that protrudes past the cusp.

Reproductive system: The arrangement of reproductive organs is triaulic (Figure 4). The straight, saccate ampulla narrows distally from the ovotestes, and bifurcates into the short oviduct and elongate vas deferens. The proximal portion of the vas deferens is thin, prostatic, and highly convoluted. More distally it becomes muscular, forming the ejaculatory segment. The distal end of the vas deferens expands and enters the wide muscular penial sac. The oviduct is short and enters the female gland mass below the bursa copulatrix. The bursa is thin-walled and joins the muscular, recurved receptaculum seminis. Just distal to the junction of the bursa and the receptaculum is the thin, slightly convoluted uterine duct, which enters the female gland mass. A large, ramified vestibular gland is present in the paratype specimen. The holotype is less mature and has a much smaller, but structurally identical vestibular gland.

Distribution: This species has only been found on the Pacific offshore islands of central Baja California: Isla Cedros and Islas San Benito. All known records are subtidal, between 13 and 23 m deep (deepest record in Hamann, 1984).

Discussion: *Mexichromis* ***amalguae*** is clearly placed in the genus *Mexichromis* based on its acuspidate radular teeth and a prominent vestibular gland (Bertsch, 1977; Rudman, 1984). *Mexichromis* ***amalguae*** represents the fourth species in the genus reported from the Pacific coast of North America. It most closely resembles *M. porterae* (Cockerell, 1901), but differs significantly in several aspects of its external and internal morphology. Both have a uniform bluish coloration with white or yellow longitudinal lines; however, *M. porterae* has a thin longitudinal mid-dorsal white line flanked by two mid-lateral yellow lines; the margin is rimmed with white. Although *M.* ***amalguae*** may have a single medial longitudinal cream line, no yellow mid-lateral lines extending lengthwise along the body from the rhinophores to the gills are present. It possesses a yellow rather than white marginal band.

The radular teeth also differ significantly between *Mexichromis* ***amalguae*** and *M. porterae* (Figures 5A–C). A row of vestigial rachidian teeth is present in *M.* ***amalguae*** but is entirely wanting in *M. porterae* (Figure 5A) and all other described members of the genus. The innermost lat-

Figure 2

Mexichromis ***amalguae*** sp. nov. Scanning electron micrographs. A. Jaw elements. B, C. Central region of radula of holotype from different angles, showing vestigial rachidian and inner lateral teeth. D. Central region of radula of paratype.

Figure 3

Mexichromis ***amalguae*** sp. nov. Scanning electron micrographs of radular teeth. A. Middle of half-row of holotype. B. Middle of half-row of paratype. C. Outermost lateral teeth of holotype. D. Outermost lateral teeth of paratype.

eral of *M. **amalguae*** bears a series of smaller denticles on either side of a larger central denticle, as in *M. tura* (Marcus & Marcus, 1967) (MARCUS & MARCUS, 1967:fig. 61; RUDMAN, 1984:figs. 70A, B). In *M. porterae* (Figure 5A; BERTSCH, 1978:figs. 55, 56; RUDMAN, 1984:fig. 72A) the innermost lateral teeth are laterally flattened.

The most profound difference between the two species is in the anatomy of the reproductive system. In *Mexichromis **amalguae*** the receptaculum seminis is almost as large as the bursa copulatrix, while in *M. porterae* the receptaculum is much smaller (RUDMAN, 1984:fig. 71a; present study), as in the genus *Hypselodoris* (RUDMAN, 1984).

Mexichromis antonii (Bertsch, 1976) is immediately distinguished by its complex coloration pattern of blue, magenta, black, yellow-orange, and white; by the larger number of rows of teeth (up to 78 reported), and by the longer and greater number of denticles on each tooth (cf. BERTSCH, 1976b:figs. 5–8).

Mexichromis tura (Marcus & Marcus, 1967) has a complex series of three differently colored marginal bands and a dark dorsal center spotted with yellow dashes and dots (KERSTITCH & BERTSCH, 1988). Its proportional radular count is slightly different (42 rows, 31 teeth, versus the 24–46 rows and 22–27 teeth of *M. **amalguae***). More importantly, its teeth are shaped differently (cf. RUDMAN, 1984:fig. 70; BERTSCH, 1978:figs. 57–60).

Indo-Pacific species have entirely different color patterns and radular characteristics. *Mexichromis mariei* (Crosse, 1872) is white with orange and purple spots; the innermost lateral teeth have more denticles (5–7) than do similar teeth in *M. **amalguae*** (cf. RUDMAN, 1983:fig. 22). *Mexichromis festiva* (Angas, 1864) is white with red, orange, or reddish purple spots and marks; its teeth have fewer and longer denticles than does *M. **amalguae*** (cf. RUDMAN, 1983:fig. 23). *Mexichromis macropus* Rudman, 1983, is white with purple spots on raised tubercles with bright orange streaks around the notal rim; its radula has more rows (80–82) than does *M. **amalguae*** and the denticles on teeth from the middle of each half row are smaller (cf. RUDMAN, 1983:fig. 25) than those of *M. **amalguae***.

RUDMAN (1984) suggested that three other species may belong to the genus *Mexichromis*: an animal from Ghana reported by EDMUNDS, 1981 (discussed separately below), *Glossodoris multituberculata* Baba, 1953, and *Chromodoris kempfi* Marcus, 1971. The latter two species are immediately distinguished from *M. **amalguae*** by, respectively, a chrome-yellow body color with purple-tipped dorsal tubercles, and by the yellow-and-black-square design. The radular counts are also proportionately quite different: *G. multituberculata* has a count of 65 (30·0·30), whereas *C. kempfi* has 60 (105·0·105) (see BERTSCH, 1976a, for a discussion of the taxonomic use of radular counts).

There are several species of chromodorids occurring in the Caribbean and Mediterranean seas that have similar coloration to *Mexichromis **amalguae*** and need critical comparison. They are clearly not conspecific (not even con-

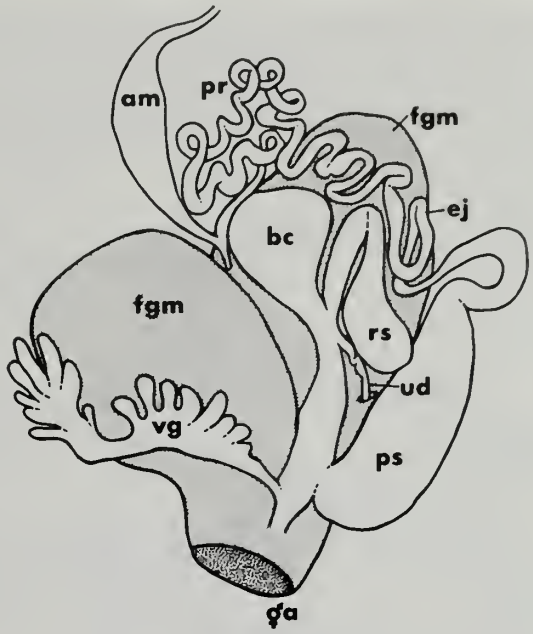

Figure 4

*Mexichromis **amalguae*** sp. nov. Reproductive system. ♀a, male-female atrium (common genital aperture); am, ampulla; bc, bursa copulatrix; ej, ejaculatory portion of vas deferens; fgm, female gland mass; pr, prostatic portion of vas deferens; ps, penial sac; rs, receptaculum seminis; ud, uterine duct; vg, vestibular gland.

generic), but the distinguishing characters must be viewed carefully.

Chromodoris nyalya Marcus & Marcus, 1967 (which may well be a species of *Noumea* Risbec, 1928), reported from the Florida Keys, has a brilliant blue body color, but the notum is margined with a bright red band. The radula is also significantly different in the shape of the teeth, the absence of a rachidian, and the radular formula (60 rows of teeth with 27 teeth in each half row; *Mexichromis **amalguae*** has only 46 rows with 27 teeth per half row).

Chromodoris purpurea (Laurillard, 1831) has a light pink body color, with dark pink, white-tipped gills and rhinophores. The notum is a plain pink, edged with orange (SCHMEKEL & PORTMANN, 1982:61). The tonal variation of pink–*purpurea* makes it necessary to compare *C. purpurea* with our eastern Pacific new species. The tonal differences are pinkish and orange versus light blue and cream yellow. The radula count of 36 rows and 25 teeth per half row is within the range of our new species, but *C. purpurea* lacks a rachidian. The tooth shapes are very different: each tooth has a *Chromodoris* cusp with 7–9 sharp, small denticles on the posterior surface of the cusp (SCHMEKEL & PORTMANN, 1982:364–365; pl. 19, fig. 5).

Chromodoris krohni (Verany, 1846) has been variously described as pink or blue, with yellow or white lines. SCHMEKEL & PORTMANN (1982:58) described a light pink

A
083100 15KV X1.20K 25.0um

B
083102 15KV X1.50K 20.0um

C
083101 15KV X2.00K 15.0um

body, dark purple gills and rhinophores, and mantle edged with yellow; there was a longitudinal yellow stripe down the middle of the back, with another (often broken) yellow line on each side between the rhinophores and gills; there may or may not be a yellow or white dorso-median line on the foot. IHERING (1880:89) emphasized a different tonal quality in the coloration: dorsum blue or rose ("*caerulescenti vel roseo*"), with three white lines down the back; golden marginal band; rhinophores purple, the five gills purple with white tips. The most obvious external difference is that *Mexichromis* ***amalguae*** may have only one dorsal longitudinal line. The radula is distinctly different, lacking a rachidian, despite the similarity of rows and tooth counts (SCHMEKEL & PORTMANN, 1982:58, cite 44 rows, 23 teeth per half row in a 10-mm-long animal; and IHERING, 1880:91, cites 30 rows, 8–10 teeth per half row in a 6-mm-long animal). Moreover, the teeth are very different from M. **amalguae**: they are distinctly *Chromodoris*-shaped, with a small cusp and up to six denticles; they lack the large, comblike denticles and the deep notch between the cusp and first denticle seen in the teeth of *M.* ***amalguae*** (cf. the illustrations by SCHMEKEL & PORTMANN, 1982: 364–365, pl. 19, fig. 3; and that by IHERING, 1880:pl. II, fig. 11).

Hypselodoris tricolor (Cantraine, 1835) is another bluish animal with a yellow or orange marginal band and longitudinal stripe. Published descriptions of this species emphasize tonal variations. SCHMEKEL & PORTMANN (1982: 67) describe a dark blue body color, with the notum edged in orange (becoming yellow or white in front of the rhinophores and behind the gills). An opaque white or yellow longitudinal line begins in front of the rhinophores and extends posteriorly, encircling the gills. There is an additional lateral line of white or yellow on each side of the medial line; it may be broken and not continuous. Rhinophores and gills are dark blue (with or without white markings). Ihering conceded that *Chromodoris tricolor* and *C. gracilis* Delle Chiaje, 1822, were similar species, but maintained them separate, identifying *C. tricolor* as having only a median longitudinal yellow line, whereas *C. gracilis* had three longitudinal yellow lines. SCHMEKEL & PORTMANN (1982) and we consider them synonymous and the characteristics to be merely intraspecific variation.

The radula of *Hypselodoris tricolor* is very different from that of *Mexichromis* ***amalguae***. Radular counts are 44 (44·0·44) (SCHMEKEL & PORTMANN, 1982:67) and 36 (35·0·35) (IHERING, 1880:65, 70), proportionately very different from *M.* ***amalguae***; it also lacks the rachidian. The shapes of the teeth are immediately distinguishable, being typically those of *Hypselodoris,* strongly bicuspid, with 3–6 small, sharp denticles on the posterior surface (not the greatly elongate denticles of *M.* ***amalguae***). The illustrations of IHERING (1880:pl. II, figs. 1, 2) and SCHMEKEL & PORTMANN (1982:364–365; pl. 19, fig. 7) of *H. tricolor* contrast with our scanning electron micrographs of *M.* ***amalguae***.

EDMUNDS (1981:195–199) identified five specimens collected in Ghana as *Mexichromis tricolor.* He was probably correct in assigning these animals to *Mexichromis* (the radula has the strong, comblike denticles characteristic of *Mexichromis*), but erroneous in assigning it to the species *Hypselodoris tricolor.* There are some subtle coloration differences, but most importantly, the radula is quite different (at the genus level) from *H. tricolor*: tooth shapes do not match, nor does the radular count of 23 (12·0·12). EDMUNDS' (1981) specimens may represent another, yet undescribed species of *Mexichromis.* Regardless, its coloration is different from that seen in *Mexichromis* ***amalguae*** (black band inside the yellow marginal band, and white longitudinal mid-dorsal line begins in front of the rhinophores), and the radula is different.

ACKNOWLEDGMENTS

We thank Paul Solonski and Bruce Heyer for collecting specimens, Bob van Syoc for helping with collecting and photographing the living animals, Jeff Hamann and David Behrens for their interest and enthusiasm in this new species, Bill Liltved for the final drawing of the reproductive system, Ann Giordano for preparing the photographic plates of our scanning electron micrographs, and Elizabeth Kools for mounting the plates. We gratefully acknowledge financial support to conduct field work from the California Academy of Sciences In-house Research Fund.

LITERATURE CITED

ANGAS, G. F. 1864. Description d'espèces nouvelles appartenant à plusiers genres de mollusques nudibranches des environs de Port-Jackson (Nouvelle-Galles du Sud), accompagnée de dessins faits d'àpres nature. Jour. Conchyl. (3)12: 43–70.

BABA, K. 1953. Three new species and two new records of the genus *Glossodoris* from Japan. Publ. Seto Mar. Biol. Lab. 3:205–211.

BEHRENS, D. W. 1980. Pacific coast nudibranchs. Sea Challengers: Los Osos, California. 112 pp.

BERTSCH, H. 1976a. Intraspecific and ontogenetic radular variation in opisthobranch systematics (Mollusca: Gastropoda). Syst. Zool. 25(2):117–122.

BERTSCH, H. 1976b. A new species of *Chromodoris* (Opistho-

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Figure 5

Mexichromis porterae (Cockerell, 1901). Scanning electron micrographs of radula of specimen from Isla San Benito Oeste. A. Central region. B. Middle of radula. C. Outermost lateral teeth.

branchia: Nudibranchia) from tropical west America. Veliger 19(2):156–158.

BERTSCH, H. 1977. The Chromodoridinae nudibranchs from the Pacific coast of America. Part I. Investigative methods and supraspecific taxonomy. Veliger 20(2):107–118.

BERTSCH, H. 1978. The Chromodoridinae nudibranchs from the Pacific coast of America. Part III. The genera *Chromolaichma* and *Mexichromis*. Veliger 21(1):70–86.

CANTRAINE, F. J. 1835. Mollusques—"diagnoses ou descriptions succintes de quelques espèces nouvelles de mollusques." Bull. Acad. Roy. Sci. Bruxelles 2(10):380–401.

COCKERELL, T. D. A. 1901. Pigments of nudibranchiate Mollusca. Nature 65(1674):79–80.

CROSSE, J. C. H. 1872. Diagnoses molluscorum Novae Caledoniae incolarum. Jour. Conchyl. (3)20:69–74.

DELLE CHIAJE, S. 1822. Atlas. Memorie sulla storia e notomia degli animali senza vertebre del regno di Napoli. 69 pp.

EDMUNDS, M. 1981. Opisthobranchiate Mollusca from Ghana: Chromodorididae. Zool. Jour. Linn. Soc. 72:175–201.

HAMANN, J. 1984. Cover photograph. Shells and Sea Life 16(9).

IHERING, H. VON. 1880. Beiträge zur Kenntniss der Nudibranchien des Mettelmeeres. 1. Malak. Blatt. N.F. 2:57–112.

KERSTITCH, A. & H. BERTSCH. 1988. *Mexichromis tura*: range extension of a rarely observed nudibranch. Veliger 30(4): 421.

LAURILLARD, C. L. 1831. *In:* Guerin Mag. de Zool. 1:17, pl. 17.

MARCUS, EV. DU BOIS REYMOND. 1971. Opisthobranchs from northern Brazil. Bull. Mar. Sci. 20(4):922–951.

MARCUS, EV. DU BOIS REYMOND & ER. MARCUS. 1967. American opisthobranch mollusks. Univ. Miami Stud. Trop. Oceanog. 6:256 pp.

RISBEC, J. 1928. Contribution à l'étude des nudibranches Néo-Calédoniens. Faune Colon. Française 2(1):1–328.

RUDMAN, W. B. 1983. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Chromodoris splendida, C. aspersa* and *Hypselodoris placida* colour groups. Zool. Jour. Linn. Soc. 78:105–173.

RUDMAN, W. B. 1984. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. Zool. Jour. Linn. Soc. 81:115–273.

SCHMEKEL, L. & A. PORTMANN. 1982. Opisthobranchia des Mittelmeeres. Nudibranchia und Saccoglossa. Springer-Verlag: Berlin. 410 pp.

VERANY, G. B. 1846. Descrizione di Genova e del Genovesato. 1(2). Regno Animale Molluschi. Pp. 90–110.

WHEELOCK, W. & H. E. GULICK. 1975. Baja California guidebook. Arthur H. Clark: Glendale, California. 232 pp.

The Veliger 31(1/2):135-140 (July 1, 1988)

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NOTES, INFORMATION & NEWS

A Record of an Echinoderm Host of *Melanella columbiana* (Gastropoda: Eulimidae)

by
Bruce J. Leighton
Department of Biological Sciences,
Simon Fraser University,
Burnaby, British Columbia, Canada V5A 1S6

On 25 October 1984, six specimens of *Melanella columbiana* Bartsch, 1917, were removed from the body surface of the aspidochirote holothurian *Stichopus californicus* (Stimpson, 1857) which had been collected by SCUBA from Howe Sound, British Columbia. The gastropods ranged in shell height from 4.0 to 6.2 mm and were found on four of seven of the sea cucumbers that were collected. They were attached by their acrembolic proboscis, which eulimids use to penetrate the body wall of their echinoderm hosts in order to feed on host body fluid (Fretter & Graham, 1962).

This species was described by Bartsch (1917) under several different names, for male, female, and young specimens (Anders Waren, personal communication). A host for *Melanella columbiana* has not previously been reported.

The identity of the gastropod was established by Dr. Anders Waren of the Department of Zoology, University of Goteborg, Sweden. Three specimens are deposited in the Swedish Museum of Natural History, Stockholm, and two specimens have been sent to the British Columbia Provincial Museum, Victoria. The author would like to thank Dr. J. Lane Cameron for his assistance in the field and Dr. P. V. Fankboner for the use of his laboratory.

Literature Cited

Bartsch, P. 1917. A monograph of west American melanellid mollusks. Proc. U.S. Natl. Mus. 53(2207):295-356, pls. 34-49.

Fretter, V. & D. Graham. 1962. British prosobranch molluscs. Ray Society: London. 755 pp.

Professor Ralph I. Smith: A Tribute to his Manuals of Marine Invertebrates and to his Academic Progeny

by
James T. Carlton
Oregon Institute of Marine Biology,
Department of Biology,
University of Oregon,
Charleston, Oregon 97420, U.S.A.

Daphne Gail Fautin
Michael G. Kellogg
Department of Invertebrate Zoology,
California Academy of Sciences,
Golden Gate Park,
San Francisco, California 94118, U.S.A.

Barbara E. Weitbrecht
Department of Ichthyology,
California Academy of Sciences
and
Armand M. Kuris
Department of Biological Sciences,
University of California,
Santa Barbara, California 93106, U.S.A.

Ralph Ingram Smith retired as Professor of Zoölogy at the University of California at Berkeley at the end of the spring 1987 semester, 41 years after his arrival on that campus in 1946. Professor Smith also stepped down in 1987 from 23 years as Secretary of the California Malacozoological Society (C.M.S.), a post he had held since 1964, when this journal was in its sixth volume. Dr. Smith has also served on the Editorial Board of *The Veliger* since 1960. His retirement from Berkeley and from the C.M.S. permits us to celebrate two of his major contributions to invertebrate zoology, including malacology: his many years of scholarly research, writing, and editorial labors, and the heritage he has created in his many students.

Professor Smith's many contributions to comparative physiology are well known internationally. Less well known, perhaps, is that Professor Smith has punctuated his long scholarly career of research and teaching with the production of two of the major guides to the marine invertebrates of the United States—the "Light's Manual" of the Pacific coast, and the "Woods Hole Manual" of the Atlantic coast.

At the time of Dr. Smith's arrival in Berkeley, Professor S. F. Light was proceeding slowly with revisions on his "syllabus"—the "Laboratory and Field Text in Invertebrate Zoology." In 1949, two years after Light's death, Ralph, along with Frank Pitelka, Frances Weesner, and Donald Abbott, began organizing the many specialists to

prepare chapters for the Second Edition of Light's syllabus. Ralph worked on the syllabus in the summers at Hopkins Marine Station, at Pacific Grove, and by 1952 he was able to write to Mrs. Mary H. Light, "after several years of work and numerous delays we expect to send to press next month a complete revision of Dr. Light's 'Laboratory and Field Text.'" Throughout the production, Ralph's great concern was that the book be *affordable* to students, a concern he voiced to Mary Light in correspondence in May 1953; 19 years later, in May 1971, Ralph was to write to Grant Barnes of the University of California Press, relative to the Third Edition, "I hope a new edition can be kept within the means of students." Ralph saw no point in producing a book that was too expensive for students to buy. The "Intertidal Invertebrates of the Central California Coast"—the final title of the book—appeared in 1954, at a cost of $5.00.

The book was well received and soon widely recognized as a major compendium. We find, threaded throughout this Second Edition, Ralph's special sense of humor. An example will suffice:

In the late 1940s an intertidal rock near Hopkins Marine Station with a peculiarly prominent proboscis-like projection became locally known as "Snadrock." "Snadrock" became a popular, albeit somewhat mysterious local figure, whose name would appear on blackboards at HMS. If we examine with a hand lens the fine (but anonymous) drawing in "Light's Manual" of a living scaphopod, *Dentalium,* we find carefully written as part of the mud ripple, apparently as a sort of artist's signature, the word "Snadrock," a name that also appears on a bookspine in a chapter head block. It is not until the Third Edition of the Manual (1975) that the caption for this drawing reveals that it was "sketched by R. I. Smith."

Only five years were to pass before Ralph, restless again to put pen to paper to organize the unorganized, began work on the now-famous "Woods Hole Manual." On the eve of New Year's Eve 1962, Ralph wrote to Dr. Melbourne Carriker that there should be a guide to the invertebrates around Wood Hole to bridge the gap between the systematist and the "ordinary biologist." Ralph explained that in the winter of 1959–1960 he "threw together existing material" on such keys and checklists of the marine invertebrates of Woods Hole as had been casually accumulated over the years at MBL, and "the results were mimeographed and issued for use in the invertebrate course." Ralph continues, "although it was my expressed hope that there would follow additions and revisions, I am mainly of the opinion that the result was a rather dull thud followed by a long near-silence." Mel Carriker seized upon the opportunity to invite Ralph to return to Woods Hole for the summer of 1963, as part of the Systematics-Ecology Program, to carry on the project and to organize the many contributors. Ralph did come to MBL that summer, and Dr. Carriker recalls that Ralph spent the summer "bending elbows and pounding on heads—it was a pleasure having him there."

Ralph returned to Berkeley, pursued the work tirelessly, and by spring 1964 the book was off to the printers—the first formal review of the marine fauna of Woods Hole since 1912. The "Woods Hole Manual"—Smith's Manual—is still the *vade mecum* in the summer courses at MBL; nothing has yet replaced it.

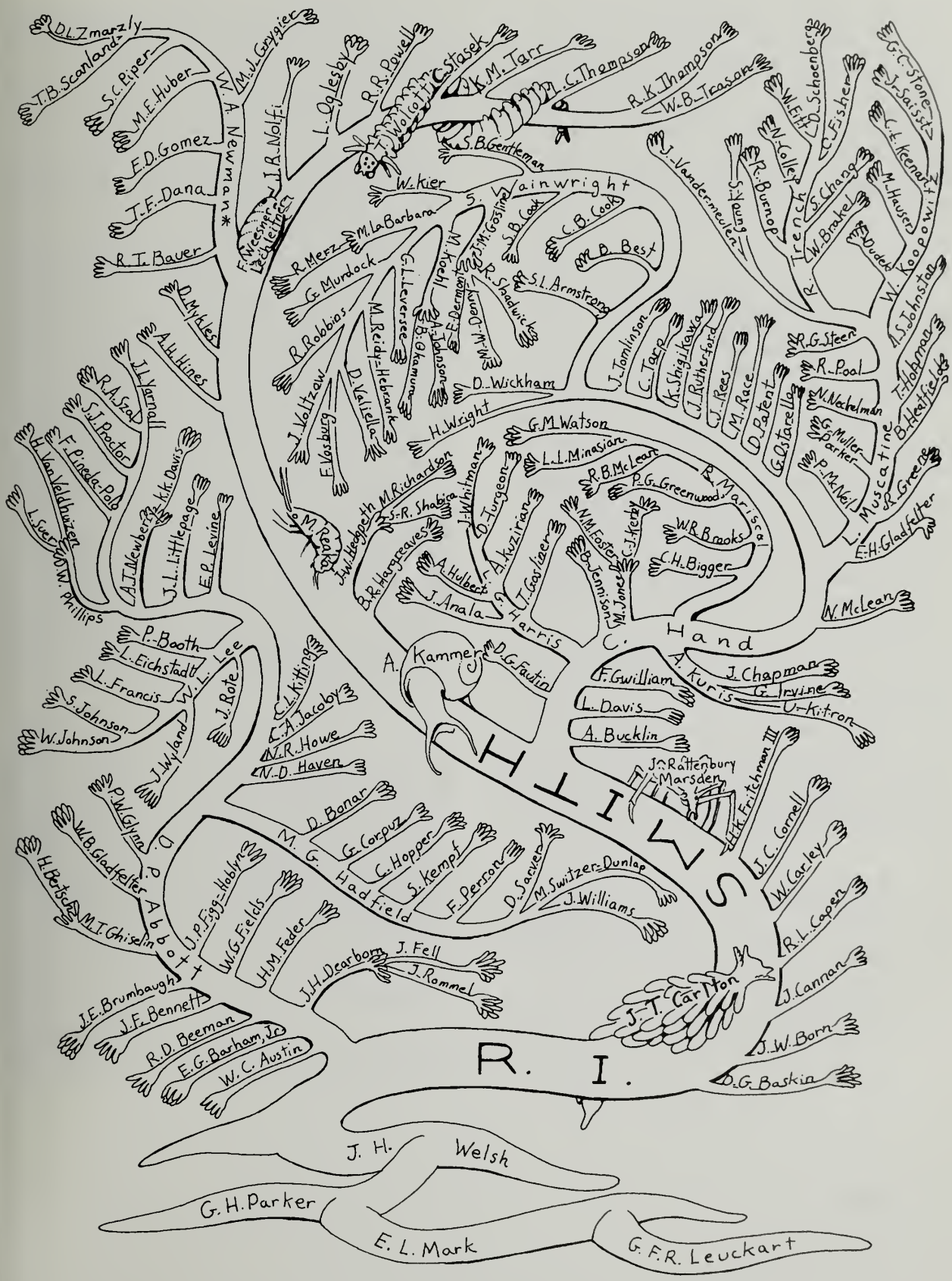
Seven years passed. Then in March 1971 Grant Barnes, of the University of California, called Ralph concerning the possibility of putting together a new edition of "Light's Manual." Ralph wrote that day "I presume it will be quite a bit of work . . . though surely not so long as the five years it took last time." A mere 72 working hours after Barnes and Professor Smith met in May to discuss details, Ralph began to send out the first letters to authors of the 1954 edition and to new contributors. The first author submitted his chapter on barnacles in July 1971, but Ralph was eventually to cajole more than 40 authors for three years, writing letters to each one, "hoping" Ralph said, "to give each one the impression that he is the only one who hasn't yet sent in his contribution."

Innumerable taxonomic complexities arise in such a work, of which Ralph sought to be a guide through the labyrinth but not the designer of the puzzle. In the spring of 1974, knowing of Ralph's now three year struggle with endless changes of names and changes of opinions, Eugene Kozloff of the University of Washington wrote to Ralph referring to him as "one of you systematists." Ralph wrote back: "I can hardly take that lying down! I am not a systematist by any stretch of the imagination, which is one reason why I work on things like the Light Manual. If I were a systematist, I would be getting everyone confused instead of trying to clarify matters, but just because I end up getting everyone confused does not of itself make me a systematist." As the manuscripts came in Ralph would not lose a moment in copy-editing, taking on matters ranging from the proper rendition of women's hyphenated maiden-married names, to whether "intertidal" was a noun, to the elimination of the umlaut over the second "ö" of "zoöid" and "zoölogy." In responding to an inquiry from one erudite contributor on the latter question, Ralph wrote: "In respect to umlauts: I realize that modern zoölogists do not spell zoölogy with an ö, and I will try to coöperate with you in deleting them."

→

Figure 1

The Ph.D.logenetic tree of Professor Ralph Ingram Smith. W. A. Newman (asterisked) is shown as a joint student of Ralph Smith and Cadet Hand. Six close academic associates are shown as epifauna along the main axis.


SMITH
R. I.
Hand
Wainwright
Newman
Abbott
Hadfield
Kammer
Welsh
G. H. Parker
E. L. Mark
G. F. R. Leuckart
D. L. Zmarzly
T. B. Scanland
S. C. Piper
M. E. Huber
E. D. Gomez
J. F. Dana
R. T. Bauer
M. J. Gaygier
J. R. Nolfi
L. Ogdesby
R. R. Powell
T. Wolotatic
C. Stasek
K. M. Tarr
L. C. Thompson
R. K. Thompson
W. B. Trason
S. B. Gentleman
W. Kier
C. B. Cook
S. B. Cook
D. Best
S. L. Armstrong
R. Shadwick
M. Gosline
M. Koch
E. Dermont
M. Donn
M. Hoch
A. Johnson
B. Okamura
M. Reidy-Hebrank
D. Valiella
D. Wickham
H. Wright
G. M. Watson
L. L. Minasian
R. B. McLean
P. G. Greenwood
R. Mariscal
W. R. Brooks
C. H. Bigger
N. M. Foster
B. Jennison
M. Jones
C. J. Kerby
T. Gosliner
A. Kuzirian
L. Turgeon
J. Whitman
M. Richardson
S. R. Shabica
B. R. Hargreaves
A. Hulbert
J. Anala
G. Harris
J. W. Hedgpeth
J. M. Read
D. G. Fautin
F. Gwilliam
L. Davis
A. Bucklin
A. Kuris
J. Chapman
G. Irvine
U. Kitron
N. McLean
E. H. Gladfelter
J. Muscatine
R. Greene
B. Heatfield
T. Hobman
A. S. Johnston
W. Koopowitz
M. Dudek
M. Hauser
C. L. Keenan
J. R. Saisset
G. C. Stone
C. D. Schoenberg
C. C. Fisher
W. E. Fitch
W. Colley
R. Burnop
S. Young
J. Vandermeulen
S. Chang
W. Brakel
R. Trench
R. G. Steer
R. Pool
V. Nickelman
G. Muller-Parker
P. McNeil
D. Patent
M. Race
J. Rees
J. Rutherford
K. Shigitowa
C. Taer
J. Tomlinson
J. Voltzow
F. Wasburg
M. Reidy-Hebrank
D. Valiella
R. Robbins
G. Murdock
R. Merz
M. La Barbara
F. Wiesner
L. Leichtman
D. Mykles
A. H. Hines
J. L. Yarnall
R. A. Szad
J. J. Proctor
F. Pineda-Polo
E. Van Valdhuizen
L. Sweeney
O. W. Phillips
A. T. Newberry
K. K. Davis
J. L. Littlepage
E. R. Levine
P. Booth
L. Eichstadt
L. Francis
S. Johnson
W. Johnson
J. Wyland
W. L. Lee
J. Rote
C. L. Kitting
C. A. Jacoby
W. R. Howe
N. D. Haven
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H. M. Feder
J. H. Dearborn
J. Fell
J. Rommel
D. Banar
G. Corpuz
C. Hopper
S. Kempf
F. Perron
D. Sarver
M. Switzer-Dunlap
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J. F. Bennett
R. D. Beeman
E. G. Barham, Jr.
W. C. Austin
J. Rattenbury
J. Marsden
H. K. Fritchman III
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W. Carley
R. L. Capen
J. Cannan
J. W. Born
D. G. Baskin

The manuscript for the book was submitted to the University of California Press in August 1973, and there followed a long year of waiting. The U.C. Press worked diligently, copy-editing and inserting hundreds of commas (that Ralph patiently removed) and touching up negatives with an artist's eye (once causing Ralph to respond "one very small animal was removed entirely—apparently mistaken for a dirt spot"). Ralph left for sabbatical to Denmark in July 1974. The matter of indexing fell to co-editor James Carlton and several colleagues. Professor Smith read the final index copy in Denmark, noting that he didn't mind "mermaid" being indexed, but "Snadrock" had to go. The Third Edition appeared in March 1975 and was the first edition actually to bear the title "Light's Manual." The gestation period had been four years.

It should be noted that Professor Smith receives no royalties from any of these books. The proceeds from the sale of "Light's Manual" go into a fund that will underwrite part of the production costs of the Fourth Edition. For his efforts for the Third Edition, Ralph received five copies of the book.

While Professor Smith's editorial productions have been impressive, equally so are the number and quality of students he has produced. As a tribute to Professor Smith's role as teacher and professor, we assembled a "Ph.D.logenetic tree" (as Ralph calls it), in the form of a colonial hydroid, with stoloniferous roots and epibiota (Figure 1). This tree was presented to Dr. Smith upon his academic retirement.

There are 176 scientists on Professor Smith's polypoid tree. Dr. Smith earned the Ph.D. in 1942 from Harvard University under John Henry Welsh, with whom he wrote *Laboratory Exercises in Invertebrate Physiology,* later revised with Ann Kammer. Welsh's own academic lineage included the American zoologist George Howard Parker, and Parker's mentor, Edward Laurens Mark, both of Harvard, and the German zoologist Georg Friedrich Rudolf Leuckart (from whom Mark earned his doctorate at Leipzig).

Professor Smith produced 22 doctoral students in his career at Berkeley. Four of these students have had students themselves, producing (as of this writing) 58 additional doctoral students. These academic grandchildren, in turn, have produced 68 more students. The latter have been the progenitors of a *fourth* generation of 18 students, for a subtotal of 144 students that Ralph calls "secondary productivity." Of the grand total of 166 students, more than a half-dozen have specialized in mollusks as the basis for their research, and all have published in *The Veliger*! (a tradition seeded by Ralph himself: *Veliger,* Vol. 1, No. 3, pp. 14–16). Also shown are six close associates, as epibionts, all of whom were strongly influenced as students or colleagues by Professor Smith.

It may be particularly noted that much of this "secondary productivity" of Professor Smith's academic doctoral descendants was based in the laboratories of Professor Cadet Hand of the University of California at Berkeley (who retired in 1985), and of the late Professor Donald P. Abbott of Stanford University (an account of whose career appears in *Veliger,* Vol. 29, No. 2, pp. 138–141, 1986). Together, they and their students have produced 134 zoologists. Both Professors Hand and Abbott long served on *The Veliger* Editorial Board, also becoming members in 1960. Along with Dr. Smith, Professor Hand also stepped down in 1987 from the C.M.S. Executive Board, of which he had served as President since its inception in 1964.

Ralph Smith has been a scholarly inspiration to more than four generations of undergraduate, graduate, and postdoctoral students in North America and Europe, students who have looked and continue to look to him for clear, precise, and logical thinking and interpretation. As one of his long-term colleagues has noted, Professor Smith is a "Practical Zoologist. First Class."

Acknowledgments

We thank Richard Eakin (University of California, Berkeley), Judy Thompson (Hopkins Marine Station), and Frances M. Okimoto (Pacific Biomedical Research Center, University of Hawaii), who provided us with the names of most of Smith's, Abbott's, and Hadfield's students, respectively. William Newman, Leonard Muscatine, and Mimi Koehl helped materially with other details as well. Shirley McArdell lettered an early draft of the tree.

Important Notice
A Change in the Timing of Volumes

For 30 years *The Veliger* has been published in a series of four-issue volumes, each volume of which spanned two calendar years—July and October of one year, and January and April of the next. While the intent was to correspond to the academic fiscal year, this original publication schedule, with its lack of synchrony between volume and calendar years, has been the continuing source of frequent confusion and misunderstanding among subscribers and authors. The governing board of the California Malacozoological Society, Inc., which publishes *The Veliger,* has recently approved shifting the publication schedule of our journal so that, beginning in 1989, each four-issue volume will be published within one calendar year.

To accomplish this one-time change, **Volume 31** will be published in two expanded issues: the present, enlarged July issue will comprise Numbers 1 and 2, and the enlarged October issue will comprise Numbers 3 and 4. Starting with **Volume 32** we will revert to volumes consisting of four separate issues as in the past, but as a result of the changes each future volume will be published within one calendar year, for example in January, April, July, and October of 1989. Billing will be moved forward to late summer–early fall to accommodate the new publication cycle and to match that of most other journals.

The price for Volume 32 will remain the same as that for the present Volume 31: $28.00 for affiliate members (individual members) and $56.00 for libraries and nonmembers. These rates include mailing to domestic addresses; add $4.00 for mailing to foreign addresses, including Canada and Mexico.

Our motivation for the change has been to better serve our valued subscribers and authors, and we trust that any short-term confusion caused by the transition will be more than offset by the long-term benefits of having our future volumes correspond to calendar years. As an additional benefit, the increased size of the July and October issues that comprise the present Volume 31 will allow us to eliminate a waiting-list of worthy papers and thus to shorten substantially the turnaround time for publishing a paper in *The Veliger.*

Thank you for your understanding. If questions arise concerning billing, or if you wish to subscribe to *The Veliger,* please write for more information to The Secretary, CMS, Inc., P.O. Box 9977, Berkeley, CA 94709, USA.

International Commission on Zoological Nomenclature

The following applications have been received by the Commission and have been published in Vol. 44 (1987), Parts 3 and 4, of the *Bulletin of Zoological Nomenclature.* Comment or advice on these applications is welcomed and should be sent to the Executive Secretary, ICZN, % British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K.

Avicula gryphaeoides J. de C. Sowerby, 1836 (Mollusca, Bivalvia): proposed conservation [involves conservation of the specific name of a fossil bivalve *Avicula gryphaeoides* J. de C. Sowerby, 1836, by suppression of the unused senior primary homonym *Avicula gryphaeoides* Sedgwick, 1829].

Haminoea Turton & Kingston, 1830 (Mollusca, Gastropoda): proposed confirmation of original spelling.

The following Opinions have been published in Vol. 44 (1987), Parts 3 and 4, of the *Bulletin*:

Opinion 1455. *Clausilia* Draparnaud, 1805 (Mollusca, Gastropoda): *Pupa rugosa* Draparnaud, 1801, designated as the type species.

Opinion 1456. *Ammonites* (currently *Euaspidoceras*) *perarmatus* J. Sowerby, June 1822 (Cephalopoda, Ammonoidea): conserved despite the senior primary homonym *Ammonites* (currently *Peronoceras*) *perarmatus* Young & Bird, [May] 1822.

The following Opinions have been published in Vol. 45 (1988), Part 1, of the *Bulletin*:

Opinion 1470. Sinuitidae Dall, 1913, Macluritidae Carpenter, 1861, and Euomphalidae de Koninck, 1881 (Gastropoda, Archaeogastropoda): conserved.

Opinion 1471. *Aplysia* (originally *Laplysia*) *viridis* Montagu, 1804 (Mollusca, Gastropoda): specific name conserved.

California Malacozoological Society

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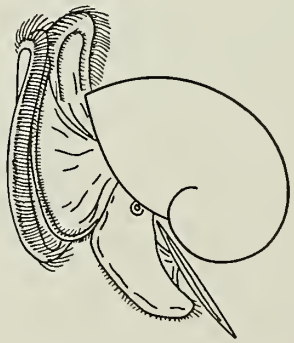

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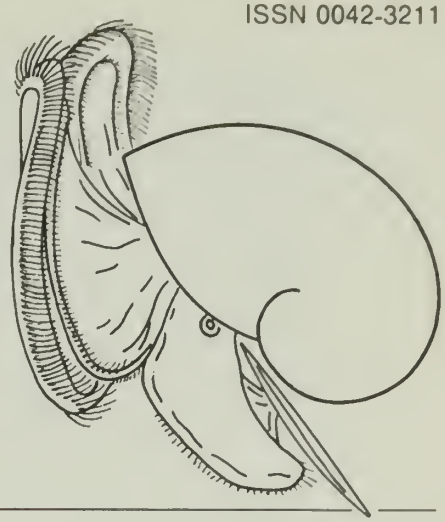

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The Genus *Chiton* in the New World (Polyplacophora: Chitonidae)

by

ROBERT C. BULLOCK

Department of Zoology, University of Rhode Island,
Kingston, Rhode Island 02881, U.S.A.

Abstract. The genus *Chiton* in the New World is reviewed. The use of scanning electron microscopy of the tegmentum and girdle scales as well as light microscopy of the radula provide valuable taxonomic features that greatly assist in the elucidation of evolutionary relationships within the genus. The use of subgenera within *Chiton s.l.* allows the distinction of discrete natural lineages within this variable polythetic taxon. *Chiton s.s.* includes: *C. tuberculatus* Linnaeus, 1758, from Bermuda and the West Indies; *C. virgulatus* Sowerby, 1840, and *C. stokesii* Broderip, 1832, from the continental shores of the tropical eastern Pacific; and *C. sulcatus* Wood, 1815, which is endemic to the Galápagos Islands. *Amaurochiton* is utilized for *C.* (*A.*) *magnificus magnificus* Deshayes, 1827, from northern Chile and a southern subspecies, *C.* (*A.*) *magnificus bowenii* King, 1832; *C. subfuscus* Sowerby, 1832, is recognized as an intergrade between the two subspecies. *Chiton* (*A.*) *cumingsii* Frembly, 1827, from Peru and Chile and *C.* (*A.*) *glaucus* Gray, 1828, from New Zealand and Tasmania are also members of *Amaurochiton*. *Diochiton* is used for: *C.* (*D.*) *albolineatus* Broderip & Sowerby, 1829, and *C.* (*D.*) *articulatus* Sowerby, 1832, from western Mexico; *C.* (*A.*) *goodallii* Broderip, 1832, from the Galápagos Islands; *C. marquesanus* Pilsbry, 1893, from the Marquesas Islands; and *C.* (*D.*) *viridis* Spengler, 1797, *C.* (*D.*) *squamosus* Linnaeus, 1764, and *C.* (*D.*) *marmoratus* Gmelin, 1791, from the Caribbean. It is noted that "*Scutigerulus* Meuschen," a name which has been associated with *C. squamosus,* has never been properly introduced. *Chondroplax* includes only *C.* (*Chondroplax*) *granosus* Frembly, 1827, from Chile. Because of their close relationship with New World species, *C.* (*D.*) *marquesanus* and *C.*(*A.*) *glaucus* are discussed for comparative purposes.

INTRODUCTION

Individuals of the genus *Chiton* Linnaeus are conspicuous members of the molluscan faunas of shallow tropical waters of the eastern Pacific, the Caribbean region, and along the western coast of South America. With the exception of *C. glaucus* from Australia and New Zealand and *C. marquesanus* from the Marquesas Islands, the many non-New World species placed in *Chiton* by various authors belong to other genera. In spite of the abundance of most New World species, the group is poorly known biologically; only *C. tuberculatus* Linnaeus, the type species of the genus, has been the subject of several biological studies. Members of the genus in the New World exhibit such diverse external morphology that one might expect this diversity to be reflected by the use of subgenera in the taxonomic literature. However, most authors have unquestioningly placed all species in the same subgenus, *Chiton s.s.* The present study was initiated to determine whether some of the marked morphological differences were indicative of natural groups of species within the genus.

The taxonomic status of New World *Chiton* has been considered by Reeve (1847), Pilsbry (1892–1894), Clessin (1903–1904), Kaas (1972), Thorpe (*in* Keen, 1971), Abbott (1974), and Kaas & Van Belle (1980). Usually in these works all New World members of the subfamily Chitoninae are placed in the genus *Chiton* and only occasionally are subgenera used. For example, in the only comprehensive monographic study of the last century, Pilsbry (1893) considered most species in question as *Chiton,* but within the genus he isolated a few species as "Section *Radsia* Gray." A few authors, including Kaas & Van Belle (1980), allocated some eastern Pacific species to the subgenus *Radsia* on the basis of increased slitting of the insertion plate.

During the investigation it became evident that some

traditional phylogenetic characters, such as slitting of the insertion plate, must be used with caution. Use of "*Radsia*" in the traditional sense was found to be undesirable, although *Chiton barnesii* Gray, 1828, the type species of *Radsia,* is sufficiently different from other species of *Chiton* that *Radsia* should be removed from *Chiton s.l.* and used as a generic name for *C. barnesii* from western South America and *C. nigrovirescens* Blainville, 1825, from South Africa (BULLOCK, 1988). Other morphological characters, for example tegmental and girdle scale surfaces as studied using scanning electron microscopy, afford a number of new and phylogenetically useful characters. Results of the present study suggest the advantage of dividing the genus *Chiton* in the New World into four subgenera in order to recognize discrete lineages within *Chiton s.l.* The relationships among the genus *Chiton,* the subgenera within *Chiton,* and other groups that are considered here to be closely related, such as *Rhyssoplax* Thiele, 1893, *Mucrosquama* Iredale & Hull, 1926, *Tegulaplax* Iredale & Hull, 1926, *Delicatoplax* Iredale & Hull, 1926, *Sypharochiton* Thiele, 1893, and *Radsia* Gray, 1847, remain an important topic in polyplacophoran systematics.

MATERIALS AND METHODS

The major collections on which this study was based are listed below. Certain specimens were selected for more detailed studies of valve structure, esthete morphology, and girdle scale structure. Methodology for preparing valves, girdle scales, and radulae for study using the scanning electron microscope (hereafter SEM) was essentially that developed by SOLEM (1972) for land snail radulae and reported elsewhere for chitons (BULLOCK, 1985). Specimens selected for SEM study were cleaned, mounted, coated with carbon and 60% gold : 40% palladium in a Denton DV-502 evaporator. Much of the SEM work was accomplished on an ISI MSM-3 located in the Department of Zoology, University of Rhode Island; some preliminary work was done on a Cambridge S-4 Stereoscan at the Graduate School of Oceanography, University of Rhode Island.

Whole or portions of intermediate valves were mounted on SEM stubs using wedges of aluminum foil and Duco cement. In order to ensure equivalency, esthete pore structure was photographed consistently in the middle of the central area near the anterior margin.

The preparation of isolated scales allowed a more precise study of scale morphology, including examination of basal structure and the ventro-lateral areas, but this method has the attendant drawback of presenting to the reader photographs of fewer scales (often a single, representative example). Isolated girdle scales are critical for examining basal structure and the ventro-lateral areas normally obscured by overlapping scales.

ABBREVIATIONS USED IN TEXT

AMNH—American Museum of Natural History, New York
AMS—Australian Museum, Sydney
ANSP—Academy of Natural Sciences of Philadelphia
BMNH—British Museum (Natural History), London
CIBM—Centro de Investigaciones de Biología Marina, Universidad Autonoma de Santo Domingo, Dominican Republic
ICZN—International Code of Zoological Nomenclature
DMNH—Delaware Museum of Natural History, Greenville
IRSN—Institut royal des Sciences naturelles de Belgique, Brussels
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge
MNHNP—Muséum national d'Histoire naturelle, Paris
NMB—Naturhistorisches Museum, Bern
NRS—Naturhistoriska Riksmuseet, Stockholm
RCB—Collection of Robert C. Bullock, Kingston, RI
RNHL—Rijksmuseum van Natuurlijke Historie, Leiden
SDSC—San Diego State College, San Diego
USNM—National Museum of Natural History, Washington, D.C.
WAM—Western Australian Museum, Perth
ZMA—Zoölogisch Museum, Amsterdam
ZMHU—Zoologischen Museum, Humboldt-Universität, Berlin
ZMK—Universitetets Zoologiske Museum, Copenhagen
ZMU—Uppsala Universitets Zoologiska Museum, Uppsala

TAXONOMIC CHARACTERS

The Shell

The shells of chitons are characteristically composed of eight separate valves, or shell-plates. Three types of valves are evident: the anterior, or head valve; the intermediate valves, of which there are six; and the posterior, or tail valve (Figures 1, 2A–D). These valves are held firmly in place by the encircling girdle (Figure 1), which is specialized mantle tissue.

The uppermost portion of the chiton shell is the tegmentum, a layer that can be smooth or variously sculptured. The entire anterior valve and the post-mucronal slope of the posterior valve, called terminal areas, have sculpture similar to that of the lateral triangle (Figures 2A, B, D).

The layer beneath the tegmentum is the highly inorganic articulamentum. The articulamentum adds strength to the valves and is the portion of the shell that composes the apophyses and insertion plates. Pectination of the teeth on the insertion plate, or that part of the articulamentum that protrudes into the encircling girdle (Figures 2A–D), has been used by many authors as the sole character defining the Chitonidae, but some other chiton groups have insertion teeth that are slightly grooved to truly pectinate.

The slitting of the insertion plate has been used as a taxonomic character by some workers, and the practice, at least in some form, is present in modern polyplacophoran literature. The intermediate valves of most *Chiton* species

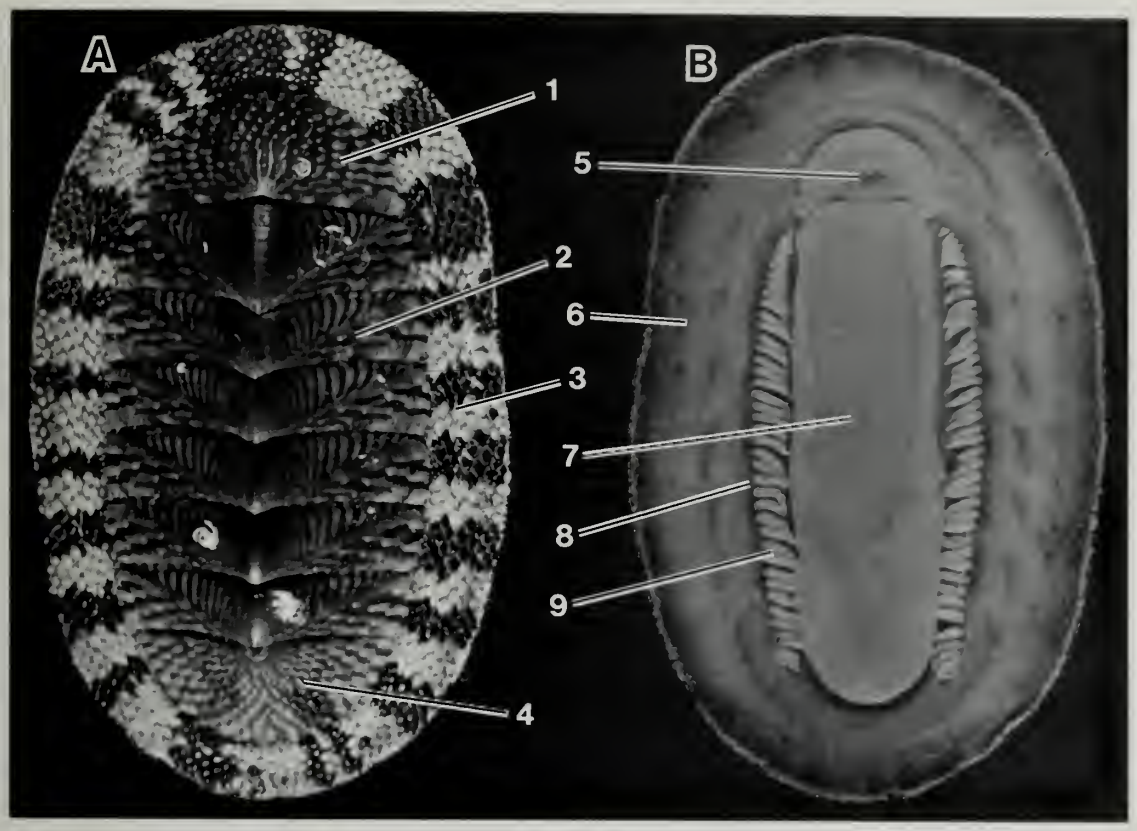


Figure 1

Dorsal and ventral views of *Chiton tuberculatus* Linnaeus. A: Dorsal view showing the shell-plates and girdle. B: Ventral view showing the foot, branchial cavity, ctenidia, and girdle. Key: 1, anterior valve; 2, intermediate valve; 3, girdle (with scales); 4, posterior valve; 5, mouth; 6, girdle; 7, foot; 8, branchial cavity; 9, ctenidia.

have a single slit per side (Figure 2C, right side), but individuals can be found that possess two slits per side on one or more valves (Figure 2C, left side). The exception is the group of *Chiton* from the tropical areas of the eastern Pacific, the members of which often have more than one slit. Gray (1847b) introduced the genus *Radsia* for *Chiton barnesii* Gray; the major diagnostic character presented was the multiple slitting of the insertion plate. Later authors have continued to use "*Radsia*" as a subgenus for these eastern Pacific chitons, in spite of the fact that *Radsia* should be used as a generic name for a distinct group of chitons that exhibits a number of ancestral characters (Bullock, 1988). The slit formula for a chiton with 18–19 slits on the insertion plate of the anterior valve, one (but occasionally two) slits on each side of each intermediate valve, and 18–20 slits on the posterior valve would be presented as 18–19/1(2)/18–20. The formula for each species studied is given as part of the description.

Ventrally, chiton valves exhibit slits, or esthete pores, one means by which the nervous tissue is able to penetrate the shell (Figure 2C). These oblong slits are usually localized in the jugal region or along the primary slit-ray, which projects from the mucro, or apex, to the slit in the insertion plate; in species having more than one slit per side, there are additional primary slit-rays. A secondary slit-ray, located along the posterior margin of the intermediate valves, is often not as well developed as the primary slit-ray, and it may be lacking or appear as a field of irregular pores.

Much of the shell nerve tissue, the esthete system, is found dorsally in the tegmentum (Figures 3–6). In the dorsal portion of this layer, or suprategmentum, esthete canals are vertical, extending to the esthetes (photosensory endings). Beneath the suprategmentum is the more inorganic subtegmentum, which contains horizontal canals that lead to the mantle. In some species these major layers may be divided. The outer margins of the tegmentum, which are contiguous with mantle tissue, are abrupt and have been referred to by a number of authors as the "eaves." "Spongy eaves" indicate that the tegmentum has large pores; the eaves are considered "not spongy" if only small pores are present. The use of this term is questionable owing to the variation observed among species. However, owing to the species-specific arrangement, size, and abundance of the horizontal canals, an SEM illustration of the anterior tegmental edge of an intermediate valve of each species studied is presented. This aspect of shell morphology is easily observed by the use of light microscopy.

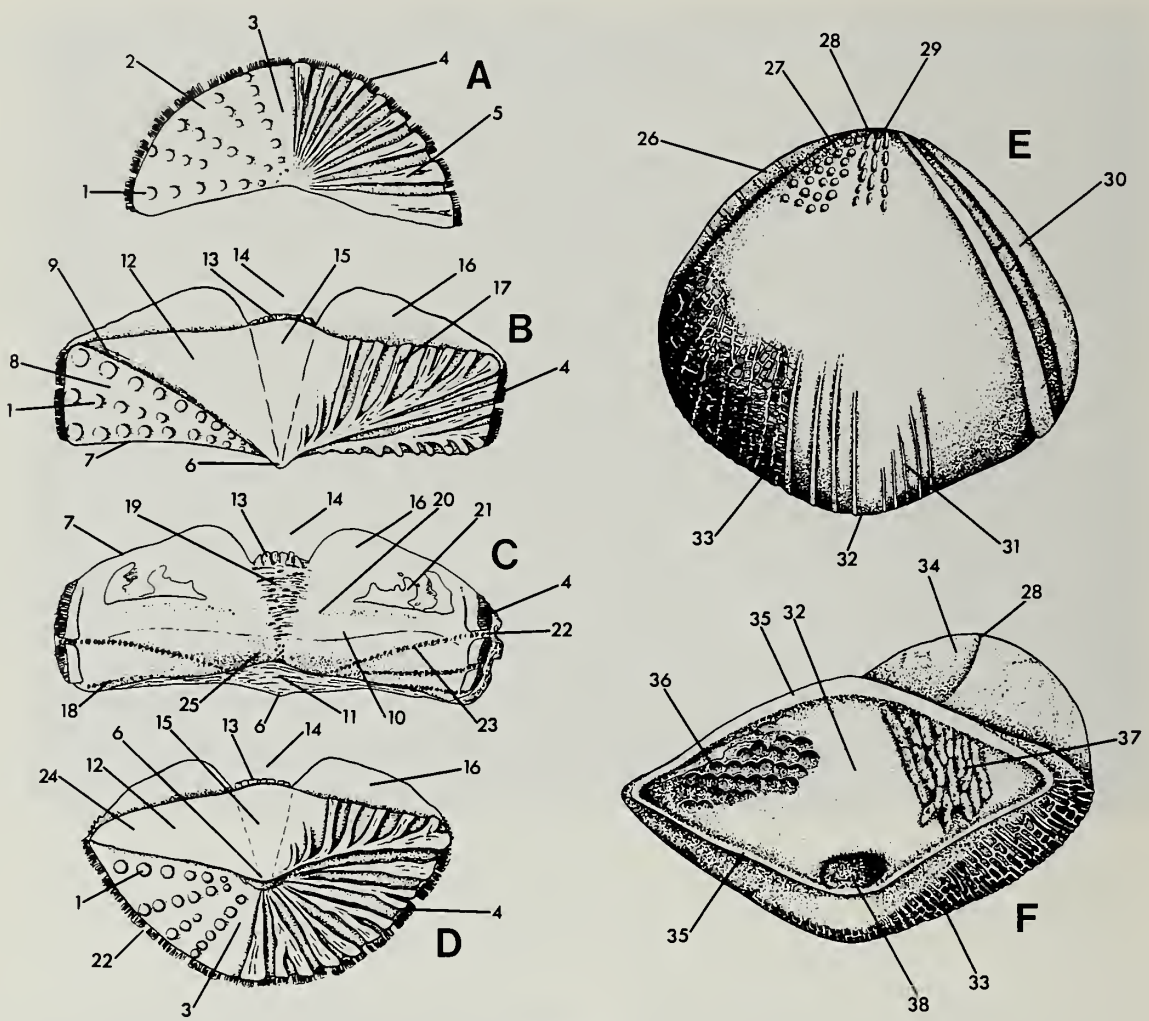


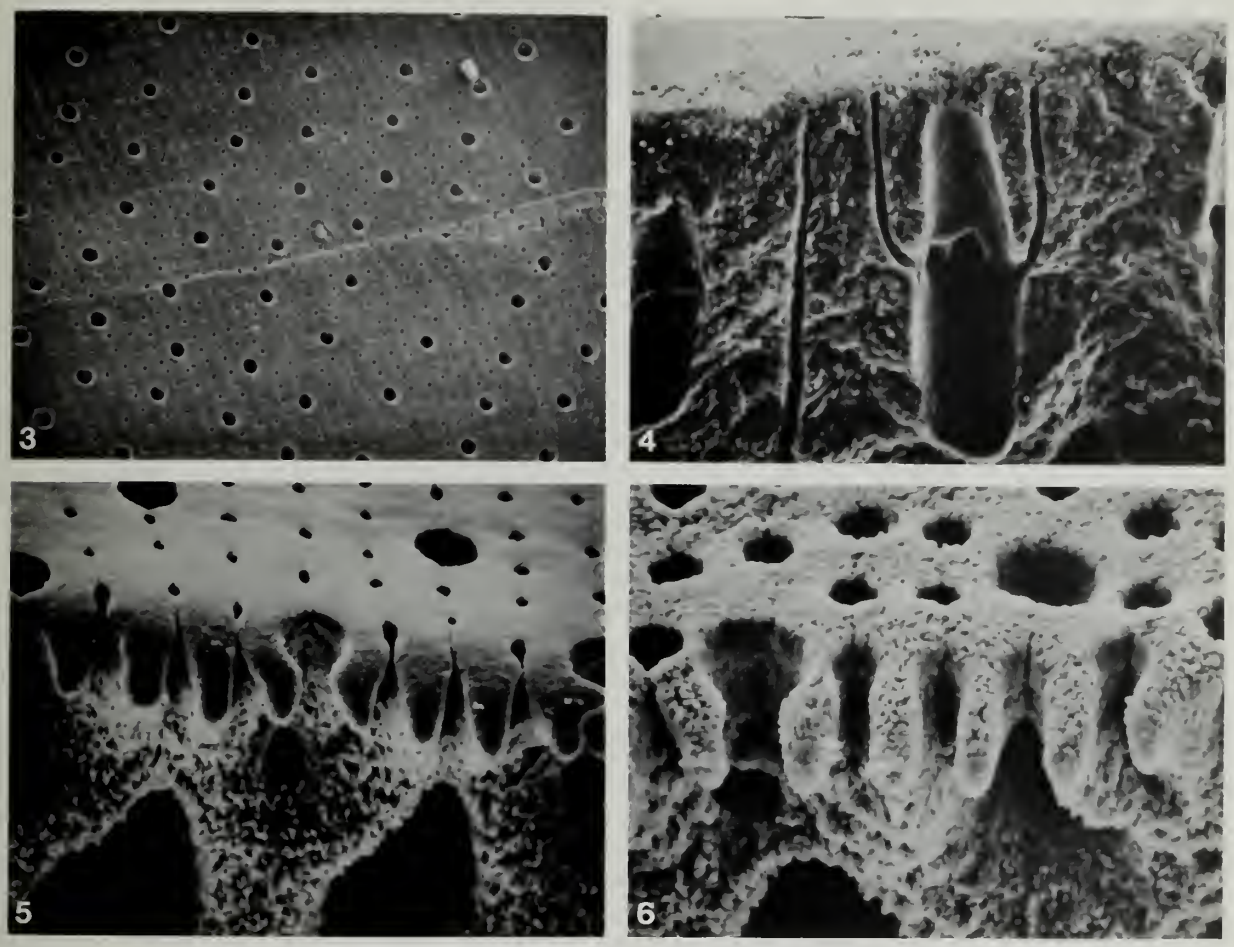
Figure 2

Semidiagrammatic illustrations of a composite *Chiton,* showing shell and girdle scale morphology. A: Anterior valve, dorsal view. B: Intermediate valve, dorsal view. C: Intermediate valve, ventral view. D: Posterior valve, dorsal view. E: Girdle scale. F: Girdle scale, basal view; Key: 1, nodule (arranged in a radial row); 2, anterior valve; 3, terminal area; 4, pectinate tooth of insertion plate; 5, radial rib; 6, mucro (intermediate valve mucro called "apex" or "beak" by many authors); 7, intermediate valve; 8, lateral triangle; 9, diagonal line; 10, central callus; 11, ventral tegmental callus; 12, central area; 13, jugal plate (with jugal teeth); 14, jugal sinus; 15, jugum (or jugal tract); 16, apophysis; 17, longitudinal rib of central area; 18, secondary slit-ray (with ventral esthete pores); 19, jugal tract (with ventral esthete pores); 20, anterior depression; 21, muscle scars; 22, slit in insertion plate; 23, primary slit-ray (with ventral esthete pores); 24, posterior valve; 25, posterior depression; 26, apical shelf; 27, apical pustule; 28, apex; 29, elongate apical pustule; 30, rib; 31, striation; 32, base; 33, reticular sculpture of ventro-lateral area; 34, medial (inner) surface area; 35, basal margin thickening; 36, scalloping; 37, irregular basal folds; 38, basal depression.

The angle of the shell-plates varies greatly among the Polyplacophora. Chiton systematists use this feature as part of a general description of shell morphology, although it is difficult to make precise angle measurements because of allometric growth and the tendency for the valves to be gambrel-shaped. In most chitons the valves of immature specimens are flatter than those of adults. The gambrel shape poses a measurement problem due to the two different slopes on each side. In all cases, the valve angle was estimated by determining the angle between the planes of the antero-ventral edges of the tegmentum. For this measurement, only intermediate valves were used; intermediate valves II (the first one) and VII (the last one) were excluded.

The Girdle Elements

The girdle of *Chiton* is covered by conspicuous, overlapping scales. While numerous authors have observed the scales of many species to be smooth, glossy, or weakly



Explanation of Figures 3 to 6

Esthete pores and anterior tegmental margin of *Chiton*.

Figure 3. Dorsal view of intermediate valve surface of *Chiton marmoratus* Gmelin, Isla Verde, Punta Mantilla, Portobelo, Panama, showing megalopores and the much smaller micropores. Some growth lines are visible (RCB) (×168).

Figure 4. *Chiton articulatus* Sowerby, Acapulco, Mexico, showing smaller micraesthete tubules arising from larger megalesthete (RCB) (×588).

Figure 5. *Chiton marmoratus* Gmelin, Isla Verde, Punta Mantilla, Portobelo, Panama, anterior margin of tegmentum revealing formation of megalo- and micropores (RCB) (×588).

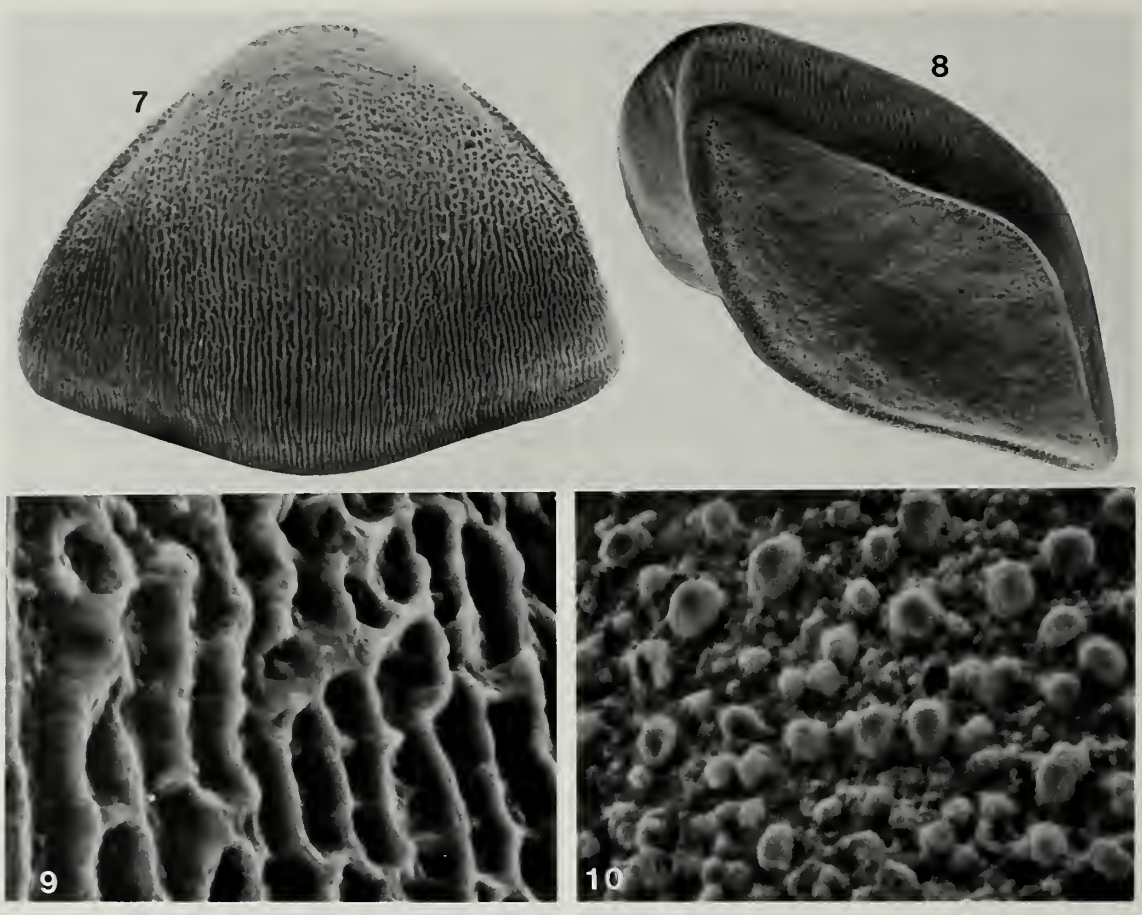
Figure 6. *Chiton viridis* Spengler, Archers Bay, St. Lucy, Barbados, anterior tegmental margin (RCB) (×840).

striated, almost all scales, in fact, have such sculptural features as pustules, ribs, and reticular sculpture (Figures 2E, F, 7–10), The sculpture in some species is typically eroded, largely owing to the presence of endolithic algae.

Among *Chiton* species, girdle scales have useful taxonomic characters that aid in species recognition and, on occasion, in the establishment of species groups. Scales on an individual specimen of *Chiton* species examined are fairly uniform, although contiguous scales of some *Rhyssoplax*, a related genus, characteristically possess different sculptural features. *Chiton* species exhibit a wide range of variation in scale sculpture, and subtle differences may be difficult to detect using light microscopy. The use of a scanning electron microscope eliminates these problems.

Precise descriptions of scales are necessary in order to compare them properly with those of closely related species. For example, the term "scales striated" means very little because of the differences in striation noted in a number of species: scales can be weakly or deeply striated, partially or completely striated; the striae can be thick or thin. Some striae are beaded, others smooth. The apex of each scale can be striated, beaded, or with irregular granules or pustules. Apical granules or pustules are present in most Chitoninae species. The reticular sculpture of the latero-ventral areas (Figure 9) is a useful taxonomic character so far as its absence or presence is concerned. Most *Amaurochiton*, a subgenus of *Chiton*, lack this reticular sculpture, although it is found in *C.* (*A.*) *glaucus* Gray, 1828.

The base of each scale is usually somewhat concave, probably affording increased surface area for attachment



Explanation of Figures 7 to 10

Girdle scale morphology of *Chiton stokesii* Broderip, W side of Isla Taboga, Bay of Panama (RCB).

Figure 7. Entire scale, exterior view (×94).

Figure 8. Basal view of scale showing basal depression (×101).

Figure 9. Reticular sculpture of ventro-lateral area (×955).

Figure 10. Apical pustules (×877).

(Figure 8). Some species exhibit additional basal features, such as a concavity near the outer margin or various types of ridges (Figure 2F). In some non-*Chiton* species, such as *Tegulaplax hululensis* (E. A. Smith) and *Rhyssoplax barnardi* (Ashby), the basal concavity is situated at the margin and can be seen in a lateral view of the scale.

All *Chiton* also have a marginal fringe of spicules. Their absence or damaged state in much of the material available for study resulted in their exclusion from consideration as phylogenetic characters. However, a few authors, including Righi (1968) and Kaas (1972), have studied the marginal spicules of some species.

The Radula

Although widely used in gastropod systematic studies, the radula has been ignored by many chiton authors. Recent investigators, especially Ferreira and Kaas, have provided outline drawings of some radular teeth, but the varying orientation of the teeth (usually the major lateral tooth) makes it difficult to use these drawings for comparative purposes. Chiton radulae usually have 17 teeth per row (Figure 11). In *Chiton* all the teeth are substantial elements and usually visible under the light microscope; most function as supporting elements (Figure 17).

The complexity of the radular teeth led Yakovleva (1952) to concentrate her studies on only three of the teeth: central, centro-lateral, and the major lateral, especially the denticle cap of the latter. The central tooth of *Chiton* is usually quite narrow, but some species have a rather broad central tooth (*e.g., Chiton stokesii* Broderip [Figures 12, 13] and *C. granosus* Frembly). Distally the central tooth is cupped (Figure 13). The centro-lateral tooth of *Chiton* has a "scraping" edge perpendicular to the anterior-posterior axis of the animal (Figures 12, 14).

The major lateral tooth is the dominant tooth of the radula, not only because of its size and complexity, but also because it possesses a conspicuous black denticle cap,

which is the major scraping element of the radula. The "wing" of the major lateral tooth (Figures 11, 15, 16) is a complicated and sometimes extensive structure whose function is unknown. Most of the remaining radular teeth function in a supporting role and they are characterized as basal plates with surfaces that articulate with contiguous teeth of the same row and teeth of the same column.

Many characteristics of the chiton radula are of taxonomic value, but I have concentrated my efforts in three areas: (1) orientation of the distal "scraping" edge of the centro-lateral tooth; (2) the denticle cap of the major lateral tooth, the most conspicuous and most easily studied element of the entire chiton radula; and (3) the angle of the denticle cap with respect to the main axis of the major lateral tooth. The complexity of the radula will certainly be explained by its functional morphology, *i.e.*, the use of the radular teeth during the various stages of the feeding process.

The denticle cap is characterized by not only its size, but its black color. TOMLINSON (1959) first reported that the black substance was magnetic. Detailed X-ray diffraction studies by LOWENSTAM (1962, 1967) revealed this substance to be composed chiefly of the mineral magnetite, as well as quantities of lepidocrocite and an apatite mineral, each forming discrete micro-architectural units. Furthermore, LOWENSTAM (1967) noted that the distribution of these minerals was "species defined" (Figure 18).

Most species of Chitoninae, as well as some other chitons, have a conspicuous black "tab" on the distal end of the back of the denticle cap (Figures 15, 18). Within the Chitoninae, a conspicuous black tab may be absent (*Radsia*), elongate (some *Chiton*), or round (other *Chiton* and *Rhyssoplax*). These differences are useful phylogenetic characters.

The Esthete System

In all individuals of Polyplacophora there are two basic types of esthetes. The larger ones are called megalesthetes; the smaller ones, termed micraesthetes, branch from the megalesthetes (Figure 4). The scanning electron microscope has proven to be an invaluable tool in the study of the polyplacophoran esthete system, especially the externally visible esthete pores. *Chiton* species present a variety of esthete pore arrangements. Regardless of the value of esthete pore patterns in the higher classification of the Polyplacophora, as species characters they are often useful, and in the present report the esthete pores of all New World *Chiton* are illustrated. The major drawback to this type of study is the required use of the scanning electron microscope for an external view. However, as Leloup's publications document, much information can be gained, and with less effort, by a study of decalcified valves using a standard compound microscope.

SYSTEMATIC TREATMENT

Class Polyplacophora Gray, 1821
Order Neoloricata Bergenhayn, 1955
Suborder Chitonina Thiele, 1931

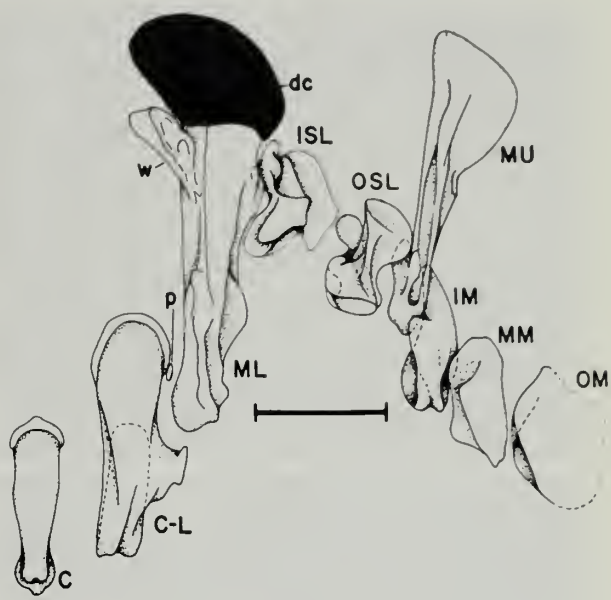


Figure 11

Right side of a single row of radular teeth of *Chiton marmoratus* Gmelin, Cabo Rojo Lighthouse, Puerto Rico (RCB). Key: C, central tooth; C-L, centro-lateral tooth with pad (p); IM, inner marginal tooth; ISL, inner small lateral; ML, major lateral tooth with wing (w) and denticle cap (dc); MM, middle marginal tooth; MU, major uncinus; OM, outer marginal tooth; OSL, outer small lateral. Scale bar = 200 μm.

Family CHITONIDAE Rafinesque, 1815

Description: Small to large in size, reaching 132 mm in length, with tegmental sculpture varying from smooth or granulose to strong concentric or, more often, radial sculpture. Apophyses broad, moderately extended, usually more so medially; jugal sinus trapezoidal; jugal plate grooved to form a number of teeth which are often indistinct. Intermediate valves with one to three slits per side; insertion teeth unevenly grooved to deeply pectinate, occasionally smooth. Tegmentum with two to three layers, the ventralmost often with a weakly developed shelf overhanging the subtegmentum, which may be greatly reduced or with up to several layers of canals. Central depression typically with numerous transverse slits in jugal tract. Primary slit-ray usually present, with circular to longitudinally elongate slits. Secondary slit-ray often evident. Girdle smooth, with numerous small spicules, or with well-developed spines or scales. Tegmentum with or without true eyes. Major lateral tooth of radula nearly always with a shovel-like denticle cap that has a single cusp, only occasionally with more than one cusp.

Remarks: Most authors have characterized the Chitonidae solely on the basis of the presence of the pectinate insertion teeth. A single-character taxonomic scheme often provides an unsatisfactory classification. Hypothesizing that pectination arose but once necessarily implies that there has

Explanation of Figures 12 to 17

Scanning electron micrographs of radular teeth of *Chiton stokesii* Broderip, Punta Mala, Panama (RCB).

Figure 12. From bottom to top: central and centro-lateral teeth, with portions of major lateral teeth visible at top. Note the clearly visible pad on the lateral margin of the centro-lateral tooth cusp (×84).

Figure 13. Central tooth (×167).

Figure 14. Centro-lateral tooth, lateral view. Note the pad, projected toward viewer, and complex folding of shaft (×334).

Figure 15. Distal end of major lateral teeth, showing denticle caps, each with a granular tab, and wings (×167).

Figure 16. Major lateral teeth, the one at the bottom fractured to show clearly the attachment of the wing to the tooth itself (×167).

Figure 17. View of a portion of the radula showing, from right to left, part of the major lateral tooth, inner small lateral tooth, outer small lateral tooth, major uncinus (only the basal part visible), inner marginal tooth, and the middle marginal tooth (×167).

been considerable subsequent modification of girdle elements, since it has placed together groups possessing well-developed girdle scales with those having spines or lacking scales. SMITH (1960) presented a conservative classification scheme for the Chitonidae, bringing into synonymy all previously proposed subfamilies, based on his opinion that species relationships within the family were still not well known. VAN BELLE (1978, 1983), KAAS & VAN BELLE (1980), and others have not always adhered to SMITH's (1960) conclusions. Unfortunately, such features as shell morphology, shell microstructure, girdle elements, esthetes, the radula, and other anatomical aspects have yet to provide a satisfactory natural classification. However, certain combinations of character traits do indicate that the genus *Chiton* and its close relatives, such as *Rhyssoplax, Tegulaplax,* and *Sypharochiton,* should be separated from other members of the family as now constituted to form the subfamily Chitoninae. The absence of esthete eyes, the presence of well-developed girdle scales, non-granular tegmentum, a shovel-like radular denticle cap generally lacking evidence of secondary cusps, and the fact that the insertion teeth of the posterior valve are not directed anteriorly, characterize the subfamily, but only the form of the radular denticle cap is unique to the Chitonidae.

Subfamily Chitoninae

Description: Animal small to large. Insertion teeth deeply pectinate to faintly grooved; insertion teeth of posterior valve not directed forward. Girdle with closely overlapping scales, concentrically arranged, striated or smooth, with or without apical granules or pustules. Shell eyes not well developed.

Remarks: The genera of the Chitoninae are characterized by morphological features of the radula, the esthete pore pattern, and the shape of the animal. Previous use of external shell morphology alone resulted in an artificial classification owing to the great plasticity of shell features within most of these groups. IREDALE & HULL (1926, 1932) presented additional subfamily names for some groups that they considered to be related to the Chitoninae: Rhyssoplacinae, Amaurochitoninae, and Sypharochitoninae. These nominal subfamilies are herein considered to be synonymous with the Chitoninae. With the exception of the lack of subfamily taxa, I generally concur with the treatment of SMITH (1960) in the *Treatise on Invertebrate Paleontology. Squamopleura* Nierstrasz, 1905, however, must be excluded as a close relative of *Chiton.* As SMITH (1960) noted, the insertion teeth of the posterior valve project anteriorly, the jugal plate is reduced and smooth, and the girdle scales do not imbricate; these traits are characteristic of the Acanthopleurinae, not the Chitoninae, as THIELE (1929) recognized. In addition, *Squamopleura* has true shell eyes, another feature of the Acanthopleurinae. The type species of *Squamopleura* is not *Chiton miles* Pilsbry, 1893, by subsequent designation of PILSBRY (1893), as SMITH (1960) and FERREIRA (1986) stated, but *Squamopleura imitator* Nierstrasz, 1905, by monotypy, as noted by VAN BELLE (1983). FERREIRA (1986) erroneously considered *Squamopleura* a junior synonym of *Acanthopleura* Guilding, 1829.

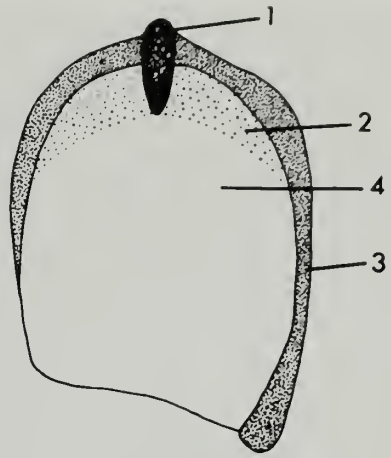


Figure 18

Semidiagrammatic illustration of the back surface of the denticle cap of *Chiton,* showing the distribution of micro-architectural units. Key: 1, tab (black), composed of magnetite, granular in appearance; 2, orange-red material (lepidocrocite); 3, black margin (magnetite), smooth in appearance; 4, yellowish area (an apatite material). Modified from LOWENSTAM (1967).

Genus *Chiton* Linnaeus, 1758

Chiton LINNAEUS, 1758:667. Type species by subsequent designation of DALL (1879), *Chiton tuberculatus* Linnaeus, 1758.

Lophyrus "Poli" H. & A. ADAMS, 1854 [in part]:469. *Non Lophyrus* Poli, 1791.

Gymnoplax "Gray" of authors [in part; in synonymy with *Chiton*].

Description: Animal large, attaining a length of 123 mm. Valves rather flattened to elevated and carinate. Tegmental structure highly variable, subtegmentum poorly to highly developed. Girdle scales variable in shape and size, smooth or variously sculptured with longitudinal striations, fine reticular sculpture, pustules, or irregular granules. Denticle cap of major lateral tooth of radula shovel-like, blunt, or somewhat elongate or round; angle of denticle cap greater than 90° from the axis of the tooth itself; distal edge of centro-lateral tooth perpendicular to longitudinal axis of animal.

Remarks: There is some question regarding the type species of *Chiton.* COX (1958) petitioned the International Commission on Zoological Nomenclature to accept DALL's (1879) type designation since as PILSBRY (1893) and DODGE (1952) had noted, none of the other species included by Linnaeus has been recognized. No decision ever resulted from this petition. Here I follow Cox and virtually all previous authors and accept Dall's subsequent designation of *C. tuberculatus.* PILSBRY (1893:151) concluded that "No other position on this question is reasonable or tenable."

SMITH (1960) presented a large synonymy for the genus *Chiton,* and then listed as subgenera the various generic names proposed by THIELE (1893) and IREDALE & HULL (1926), the latter in wide use by Australian and New Zealand malacologists. The results of the present investigation indicate that some changes must be made in SMITH's (1960) treatment of the genus *Chiton.* Like Smith, I recognize *Amaurochiton* Thiele, 1893, as a subgenus of *Chiton.* I also recognize *Diochiton* Thiele, 1893, and *Chondroplax* Thiele, 1893, as subgenera of *Chiton. Radsia* Gray, 1847, and *Sypharochiton* Thiele, 1893, are separate genera (BULLOCK, 1988) as are *Rhyssoplax* Thiele, and *Tegulaplax.* The status of *Delicatoplax* Iredale & Hull, 1926, and *Mucrosquama* Iredale & Hull, 1926, is uncertain, but they appear similar to *Rhyssoplax* and may be subgenera within that genus. *Typhlochiton* Dall, 1921, was shown by BULLOCK (1972a) to be a junior synonym of *Chaetopleura* (family Chaetopleuridae).

The genus *Chiton* includes a number of species groups so distinct as to demand division into subgenera. The subgenera used herein have at times been treated as genera by some authors. Their use as subgenera in this study was an attempt to: (1) organize apparently diverse lineages into groupings based on morphological similarity, and (2) reflect patterns of speciation, interspecific variation, and the "naturalness" of these groupings.

The divisions used within *Chiton* establish species groups, placing in different subgenera such dissimilar species as *C. tuberculatus* and *C. marmoratus,* the latter species never before excluded from *Chiton s.s.* The subgenus *Diochiton* is composed mainly of New World species, with species in the Panamic faunal province, the West Indian province, and the Marquesas Islands of the South Pacific. Previously, New World *Chiton* species were considered to be *Chiton s.s.,* except for the consistently poor usage of *Radsia,* and most *Chiton* species from elsewhere were generally considered to belong to *Rhyssoplax.* It is hoped that the present system, based on radular and shell morphology, will encourage more detailed investigations involving numerous biological parameters.

The synonymy of *Chiton* reflects some complex taxonomic problems resulting primarily from the fact that numerous authors during the first half of the nineteenth century insisted that nearly all chitons be placed in the large, inclusive genus *Chiton.* When it became more fashionable to employ other genera, names were readily available largely from the published works of GRAY (1847a, b) and THIELE (1893).

Some important radular characteristics differentiate *Chiton* from *Rhyssoplax.* In *Chiton,* the distal edge of the centro-lateral tooth is perpendicular to the longitudinal axis of the animal; without exception, all *Rhyssoplax* radulae examined have this distal edge parallel to the longitudinal axis. In addition, the subtegmentum tends to be more porous and the insertion plate more highly pectinate in *Chiton* than in *Rhyssoplax. Sypharochiton* and *Radsia* differ from *Chiton* by having a more granular tegmentum (*i.e.,* not smooth). The radula of *Radsia* exhibits ancestral characters not seen in *Chiton. Tegulaplax* is distinguished from *Chiton* by its elongate shape, less-developed pectination of the insertion teeth, and rounded valves with irregular concentric sculpture on the lateral triangle. The radula of *Tegulaplax* is similar to that of *Rhyssoplax,* not *Chiton.*

The genus *Chiton* is primarily a New World group. Many non-New World species placed in *Chiton* probably properly belong in *Rhyssoplax. Chiton marquesanus* Pilsbry from the Marquesas Islands, which is without doubt of New World origin, and *C.* (*Amaurochiton*) *glaucus* Gray from Australia and New Zealand occur outside the New World. Most species are found near the low tide mark, and very few occur at a depth of more than 3 or 4 m.

KEY TO THE SUBGENERA OF NEW WORLD *Chiton*

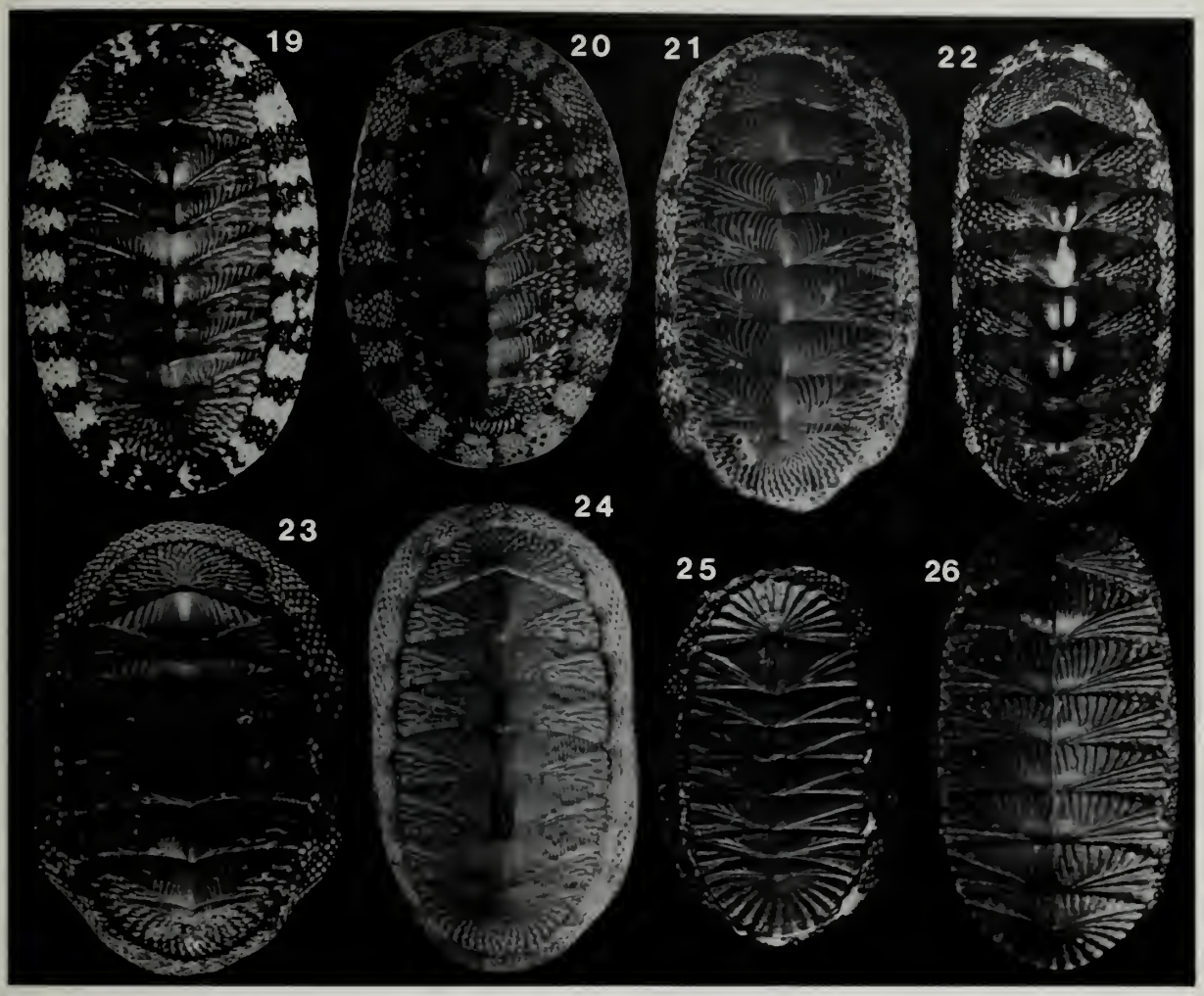
1. Terminal areas with smooth radial ribs .... *Amaurochiton*
   Terminal areas smooth, with rows of nodules, or with conspicuously bifurcating ribs 2
2. Jugum smooth ..... *Diochiton*
   Jugum with longitudinal ribs 3
3. Lateral triangle with radiating rows of large, widely spaced nodules ..... *Chondroplax*
   Lateral triangle with bifurcating ribs .... *Chiton s.s.*

Subgenus *Chiton* Linnaeus *s.s.*

Description: Animal large, attaining a length of 95 mm. Valves subcarinate. Jugum with longitudinal ribs, at least at apex; central areas with longitudinal ribs. Lateral triangle raised, with bifurcating radial ribs which may be nodular in appearance. Girdle scales generally large, lacking ribs, but with small pustules apically.

Remarks: The subgenus *Chiton s.s.* is characterized by the longitudinal ribs on the central areas and jugum, at least at the apex; the lateral triangle and terminal areas have broad, bifurcating radial ribs or radiating rows of elongate nodules which often form a checkered pattern. The subtegmentum is usually well developed, although in *C. stokesii* it is not developed and lacks the porosity of other *Chiton s.s.* Species included in *Chiton s.s.* are: *C. stokesii* Broderip, 1832, and *C. virgulatus* Sowerby, 1840, from the tropical eastern Pacific, *C. sulcatus* Wood, 1815, from the Galápagos Islands, and *C. tuberculatus* Linnaeus, 1758, from the West Indies and Bermuda. *Chiton sulcatus* Wood has been reported from the Pleistocene of the Galápagos Islands (SMITH & FERREIRA, 1977) and *C. rossi* Smith *et al.,* 1968, from the Upper Cretaceous of Puerto Rico (SMITH *et al.,* 1968).

In general, the various subgenera used in the present treatment of *Chiton* all differ from *Chiton s.s.* owing to a small number of morphological features of the shell. These subgeneric names were introduced originally by THIELE



Explanation of Figures 19 to 26

Shells of *Chiton tuberculatus* Linnaeus and *Chiton sulcatus* Wood.

Figure 19. *C. tuberculatus,* Bahía Fosforescente, Puerto Rico (RCB) (23 mm).

Figure 20. *C. tuberculatus,* Guantanamo Bay, Cuba (RCB) (38.5 mm).

Figure 21. *C. tuberculatus,* Gambier, New Providence Id., Bahama Ids. (MCZ) (65 mm).

Figure 22. *C. tuberculatus,* Guadeloupe (MCZ 156030) (50 mm).

Figure 23. *C. tuberculatus,* Gambier, New Providence Id., Bahama Ids. (MCZ 204301) (40.5 mm).

Figure 24. *C. tuberculatus,* Spaansche Put, Curaçao (RCB) (40 mm).

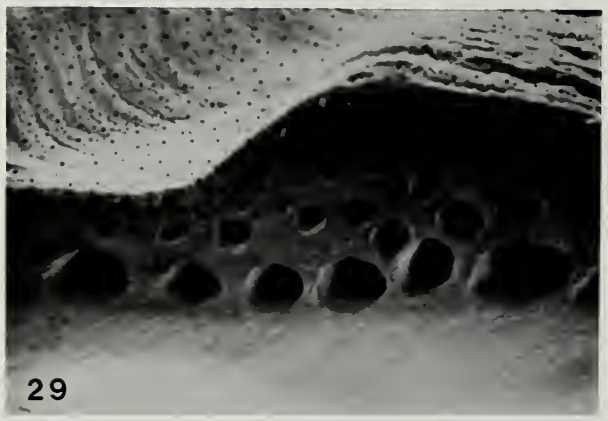
Figure 25. *C. sulcatus,* Galápagos Ids. (MCZ 83917) (15 mm).

Figure 26. *C. sulcatus,* Isla San Cristobal, Galápagos Ids. (MCZ 204339) (38 mm, slightly curled).

(1893) based on differences in radular morphology. Many of the polyplacophoran names proposed by Thiele were based on misidentified specimens (Thiele, 1909). Thiele (1909, 1929) rejected the importance of many of these names, including *Amaurochiton* and *Diochiton*. In the present paper I utilize available names based on the type species and, to a lesser degree, the original diagnosis. Each of these polythetic taxa exhibits a certain amount of variation, making it difficult to place some species into a particular subgenus, and *Chiton s.s.* is no exception. *Chiton s.s.* can usually be distinguished from: *Amaurochiton* by lacking the numerous, smooth, narrow longitudinal ribs on the jugal and central areas, and not possessing the smooth girdle scales with fine ventro-lateral striae; some *Diochiton* by lacking smooth lateral triangles and terminal areas; and all *Diochiton* by lacking smooth jugal and nearly always smooth central areas. *Chondroplax* differs from *Chiton s.s* by its thick shell plates with radiating rows of large nodules on the terminal areas.

KEY TO THE SPECIES OF *Chiton s.s.*

1. Longitudinal ribs of central area fine, those near jugum bending laterally; more than 20 ribs per side in adult specimens 2



Explanation of Figures 27 to 30

Esthete pores and anterior tegmental innervation in *Chiton tuberculatus* Linnaeus and *C. sulcatus* Wood.

Figures 27 and 28. *C. tuberculatus,* entrance to Bahía Fosforescente, Puerto Rico (RCB) (Figure 27, ×327; Figure 28, ×164).

Figures 29 and 30. *C. sulcatus,* Small Pt. NE of Guy Fawkes, N end of Isla Santa Cruz, Galápagos Ids. (MCZ) (Figure 29, ×41; Figure 30, ×327).

Longitudinal ribs of central area usually coarse, those near jugum bending medially; fewer than 20 ribs per side in adult specimens 3

2. Radiating ribs of lateral triangle fine, lacking nodules; girdle scales relatively small, about 10 per width of lateral triangle; subtegmentum highly porous; girdle scales glossy ..... *C. virgulatus*

Radiating ribs of lateral triangle fine, nodular; girdle scales relatively large, about 8 per width of lateral triangle; subtegmentum not very porous; girdle scales dull ..... *C. stokesii*

3. Shell and girdle scales dark greenish brown to black; insertion plate of intermediate valve with 2 slits per side; girdle scales moderately inflated ..... *C. sulcatus*

Shell and girdle scales mottled with cream white and dull green, rarely dark greenish brown; insertion plate of intermediate valves with 1 slit per side; girdle scales moderately flattened ..... *C. tuberculatus*

Chiton (*Chiton*) *tuberculatus* Linnaeus, 1758

(Figures 1, 19–24, 27, 28, 31, 35, 38)

Chiton tuberculatus Linnaeus, 1758:667, sp. 2 (in America [type locality herein restricted to Gambier, New Providence Id., Bahama Islands]; type presumed lost); Wood, 1815:22; Pilsbry, 1893:153, pl. 33, figs. 58–60; Dall & Simpson, 1901:453; Thiele, 1910:112; Abbott, 1954: 324, pl. 1d, text fig. 67f; Usticke, 1959:90; Lewis, 1960: 391 [ecology, reproduction]; Warmke & Abbott, 1961: 219, text fig. 33a; Righi, 1968:73 [radula]; de Jong & Kristensen, 1968:29; Kaas, 1972:102, figs. 212–221, pl. 8, figs. 2, 3; Glynn, 1970:1–21 [ecology, reproduction]; Morris, 1973:281, pl. 76, fig. 9; Abbott, 1974: 405, fig. 4747; Humfrey, 1975:291; Kaas & Van Belle, 1980:135; Lyons, 1981:38; Baboolal *et al.,* 1981:40, fig. 4; Vokes & Vokes, 1983:46, pl. 49, fig. 10; Ferreira, 1985:202; Jensen & Harasewych, 1986:397, fig. 130 [in part].

Chiton squamosus of authors, *non* Linnaeus: Reeve, 1847:pl. 3, sp. 16; Shuttleworth, 1853:196; Metcalf, 1893: 249, 250; Morris, 1973:281, pl. 76, fig. 1.

Explanation of Figures 31 to 33

Girdle scales of *Chiton s.s.*

Figure 31. *Chiton tuberculatus* Linnaeus, San Juan, Curaçao (RCB) (×46).

Figure 32. *C. virgulatus* Sowerby, Bahía Kino, Mexico (MCZ 193026) (×60).

Figure 33. *C. sulcatus* Wood, Small Pt. NE of Guy Fawkes, N end of Isla Santa Cruz, Galápagos Ids. (MCZ) (×36).

Chiton undatus SPENGLER, 1797:68 (St. Croix og St. Thomas in Westindien; type in ZMK); THIELE, 1893:362, pl. 30, fig. 2 [radula].

Chiton bistriatus WOOD, 1815:7 [refers to CHEMNITZ (1785), pl. 94, fig. 788] (locality unknown [herein designated as Gambier, New Providence Id., Bahama Ids.]; location of type unknown); WOOD, 1825:1, pl. 1, fig. 2.

Chiton tessellatus WOOD, 1815:23 [refers to CHEMNITZ (1788), pl. 173, fig. 1690] (no locality given [herein designated as Gambier, New Providence Id., Bahama Ids.]; location of type unknown). *Non* Quoy & Gaimard, 1835.

Chiton squamosus, var. *obscurus* SOWERBY, 1840a:2, fig. 76 [*squamosus* var. on p. 10] (West Indies; location of type unknown).

Chiton assimilis REEVE, 1847:pl. 14, sp. 76, 77b [not 77a] (West Indies; type in BMNH? [not found]); DALL, 1879: 79, 126, pl. 3, fig. 26 [radula].

Chiton (*Lophurus*) *assimilis* Reeve. SHUTTLEWORTH, 1853: 197.

Chiton squamosus, var. *similis* PETIT DE LA SAUSSAYE, 1856: 155 [nude name].

Chiton tuberculatus, var. *ater* PILSBRY, 1893:155, pl. 33, fig. 63 (St. Kitts; Trinidad; type in ANSP [not found; DAVIS *et al.* (1979) did not record type in ANSP]).

Chiton tuberculatus, var. *assimilis* Reeve. PILSBRY, 1893:155, pl. 33, figs. 61, 62; DALL & SIMPSON, 1901:453.

Chiton (*Lophyrus*) *occidentalis* "Reeve" CLESSIN, 1903:44, pl. 16, fig. 5. *Non* Reeve.

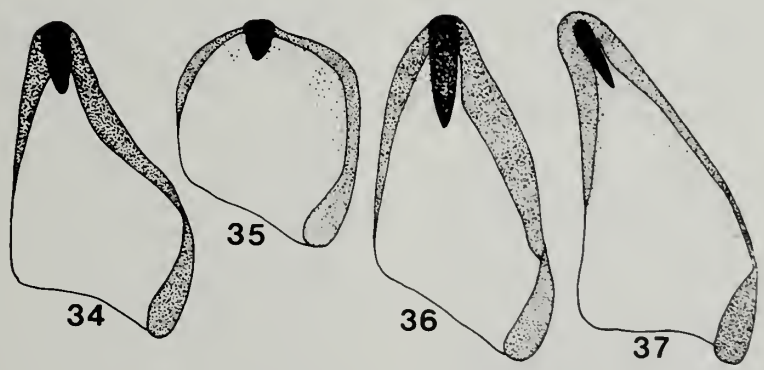
Chiton (*Lophyrus*) *assimilis* Reeve. CLESSIN, 1903:45, pl. 16, fig. 4 [not pl. 18, fig. 5, which = *C. occidentalis* Reeve].

Chiton assimilis, var. *reeveanus* CLESSIN, 1904:118, pl. 41, fig. 3 (Westindien; [Clessin gives reference to "*Chiton assimilis* var. Reeve, Conchologia Iconica, fig. 17b" (*sic*)]; type in BMNH? [not found]).

Chiton (*Chiton*) *tuberculatus* Linnaeus. THIELE, 1929:19.

Chiton tuberculata [*sic*] Linnaeus. ABBOTT, 1958:108.

Chiton tuberculatus, form *assimilis* Reeve. WARMKE & ABBOTT, 1961:219.



Explanation of Figures 34 to 37

Representative denticle caps of *Chiton s.s.*

Figure 34. *Chiton sulcatus* Wood, Small Pt. NE of Guy Fawkes, N end of Isla Santa Cruz, Galápagos Ids. (MCZ).

Figure 35. *C. tuberculatus* Linnaeus, Cabo Rojo Lighthouse, Puerto Rico (RCB).

Figure 36. *C. stokesii* Broderip, Playas del Coco, Costa Rica (RCB, *ex* Spight).

Figure 37. *C. virgulatus* Sowerby, Baja California (RCB).

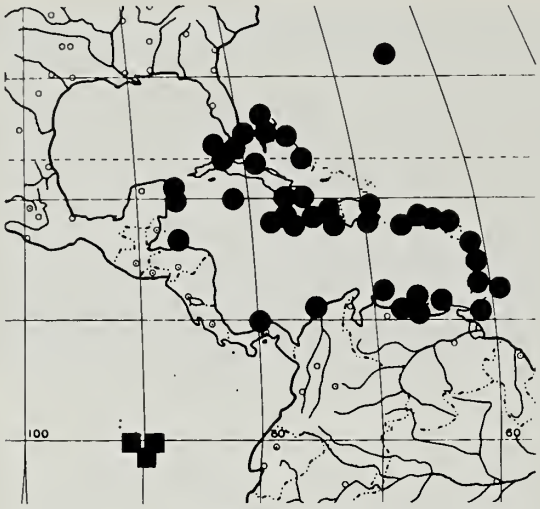


Figure 38

Distribution of *Chiton tuberculatus* Linnaeus (●) and *C. sulcatus* Wood (■).

Chiton tuberculatum [*sic*] Linnaeus. COWDEN, 1961:313; COWDEN, 1963:406.

Non Chiton tuberculatus "Linnaeus" ROMASHKO, 1984:59 [misidentification of *C. viridis* Spengler].

Description: Animal large, reaching 92 mm in length, 56 mm in width. Angle of valves about 105°. Anterior valve slightly convex; post-mucronal slope of posterior valve concave at first, remainder straight. Mucro rather sharp, anteriorly acentric on posterior valve. Jugal region smooth; central areas with irregular, dorsally smooth, longitudinal ridges which vary in number and strength. Lateral triangle raised, with five to eight irregular, nodular, anastomosing, radial ribs. End valves with numerous elongate nodules which form a checkered pattern. Shell color variable, usually white or buff with varying longitudinal streaks of dark greenish brown on the jugum; rest of shell greenish brown with raised sculpture often lighter in color. At times specimens entirely dark or gray-green. Girdle alternately banded with white or dark. Interior of shell greenish white or pale blue.

Tegmentum: Upper layer of suprategmentum lighter in color than rest of tegmentum; subtegmentum with large, close-packed canals with occasional smaller canals above. Subtegmentum reduced or absent at jugum (Figure 29).

Esthete pores: Megalopores round, about three to four times as large as round micropores (Figure 27).

Articulamentum: Central depression of intermediate valves with scattered slits oriented perpendicularly to the longitudinal axis. Primary slit-ray present in all but very mature specimens. Slit formula 12–15/1(2)/14–18.

Girdle scales: Moderate size, roundly triangular. Ventrolateral sculpture of very fine, anastomosing longitudinal ribs, becoming reticular midway to the apex. Apical region rather smooth, with some evidence of very small apical pustules. Lateral keel evident (Figure 31).

Radula: Central tooth quite narrow, distally cup-shaped, but somewhat squarish. Pad of centro-lateral tooth elongate, irregular in appearance, and directly attached to tooth. Wing of major lateral tooth elongate, pointed. Denticle cap shovel-like, slightly pointed distally; black tab not elongate. Blade of major uncinus flared with some evidence of striae distally (Figure 35).

Remarks: *Chiton tuberculatus* is easily distinguished from all other species of *Chiton* by having strong, flattened, longitudinal ribs on the central areas and especially the patchwork of nodules (rather than radial ribs) on the terminal areas. *Chiton sulcatus* Wood from the Galápagos Islands has bolder sculpture, and the longitudinal ribs of the central area occur on the entire jugum, whereas in *C. tuberculatus* this area is smooth, at least away from the mucro. *Chiton tuberculatus* could be confused with *C. viridis* Spengler, a sympatric species, but the girdle scales of the latter species are proportionately smaller, lack the lateral keel, and have small pustules on the dorso-lateral area; the valves of *C. viridis* have radiating ribs or rows of nodules on the terminal areas, the lateral triangle is raised higher, and the longitudinal ribs of the central area are finer, shorter, more irregular, and characteristically have a deep groove between them near the lateral triangle. The common, mostly sympatric *C. squamosus* Linnaeus differs by having flatter, more ovate girdle scales; radiating rows of smaller nodules; and, above all, by having a smooth central area. The color of *C. squamosus* should aid in differentiation; the rather broad streaks of light brown across the central areas and onto the lateral triangle and the distinctive brown splotches along the posterior edge of the lateral triangle easily serve to distinguish this common chiton from *C. tuberculatus*. The esthete pore patterns for each of the above mentioned species are species specific.

When one examines Central American collections, it is possible on first glance to confuse the Caribbean *Chiton tuberculatus* with the eastern Pacific *C. stokesii*. The finer longitudinal ribs of *C. stokesii* extend across the jugum, and the subtegmentum is less developed than in *C. tuberculatus*. The radulae of the two species differ considerably; in *C. stokesii* the central tooth is broad, and the denticle cap is attenuate with an elongate black tab distally on the back surface. Again, the difference in the esthete pore pattern is striking. In both species smaller micropores surround the megalopore; however, in *C. stokesii* as in *C. virgulatus* each megalopore occurs on a mound making it volcano-like. In *C. tuberculatus* the megalopores are not raised (Figure 27).

Chiton tuberculatus is one of the best known chitons in the world. It was represented in many early collections under the name "*Chiton squamosus*," another West Indian species described by Linnaeus. A great deal of intraspecific variation is exhibited by *C. tuberculatus*, as noted by PILSBRY (1893). Some examples, especially in the Greater Antilles, have strong sculpture (Figures 21, 23), while others, particularly in the southern Caribbean (Figures 22, 24), have finer sculpture.

This common West Indian species has been used in various biological studies, involving growth (CROZIER, 1918, 1919b), ethology (CROZIER & AREY, 1918, 1920; AREY & CROZIER, 1919; CROZIER, 1920), coalescence of shell-plates (CROZIER, 1919a), physiology (KIND & MEIGS, 1955; LAWRENCE, 1970; HÖGLUND & RAHEMTULLA, 1977), reproduction and development (METCALF, 1892, 1893) [as "*C. squamosus*"]; SOUTHWICK, 1939; COWDEN, 1974) and histology (COWDEN, 1963). GLYNN (1968) and MENZIES & GLYNN (1968) reported on symbiotic isopods found in the branchial cavity, and BULLOCK & BOSS (1971) noted the occurrence of the bivalve *Lithophaga* in the shell-plates. LOWENSTAM (1967) utilized *Chiton tuberculatus* in his study of the composition of polyplacophoran denticle caps. A very thorough ecological study of *C. tuberculatus* was produced by GLYNN (1970) whose results added to, and in some cases corrected, the observations of Crozier and Arey.

Chiton tuberculatus is found commonly from the lower intertidal zone down to shallow subtidal areas. It is often observed on pilings, in rock crevices and, during the day, under rocks. As GLYNN (1970) observed, *C. tuberculatus* lives on exposed wave-swept shores where it occupies part of the intertidal area below that of *Acanthopleura granulata* (Gmelin).

The reproductive period of *Chiton tuberculatus* is from October and November in Puerto Rico (GLYNN, 1970) and October to December in Barbados (LEWIS, 1960). LEWIS (1960) concluded that "The pelagic larval phase of the species is short. Metamorphosis begins as early as three days after eggs are fertilized."

Distribution: *Chiton tuberculatus* occurs from Boca Raton, Florida, and Bermuda in the north, south to Trinidad, and from Isla Mujeres, Yucatán, Mexico, to Isla de Margarita, Venezuela (Figure 38). HUTTON *et al.* (1956) recorded *C. tuberculatus* from Boca Ciega Bay, St. Petersburg, Florida, but this record, repeated by SYKES & HALL (1970), is certainly in error. Records in the literature from Texas (PILSBRY, 1893; M. SMITH, 1937) are also wrong. ABBOTT (1974) noted that this species is rarely collected at Boca Raton, Florida.

Locality records: FLORIDA: Miami Beach (DMNH); Indian Key (USNM); Bird Key, Tortugas (MCZ). MEXICO: Naval station, Isla Mujeres (USNM); intertidal rock pools, E shore, about 2 mi [3.2 km] S of N end, Isla Mujeres (ANSP); about 3 km N of S tip, Isla Mujeres (RCB); W side of Isla de Cozumel (ANSP); San Miguel, Isla de Cozumel (USNM). HONDURAS: (BMNH). PANAMA: (RNHL); at breakwater, Limon Bay (USNM); Toro Pt., ocean side; Toro Pt., bay side (both RCB); Cristobal (USNM); Colón (MCZ, IRSN); near lighthouse, Colón; Fort Randolph, Galeta Id.; Ironcastle Pt., Portobelo (all RCB). COLOMBIA: Puerto Colombia (USNM); Santa Marta (IRSN, NRS); rocky pt., N end of Rodadero Beach, Santa Marta (ANSP). VENEZUELA: Puerto Cabello (ZMHU); Caracas (ZMHU); La Guaira (RNHL, ZMHU); Playa del Agua, 1 mi [1.6 km] N of Cabo Blanco, Isla de Margarita (MCZ); just N of La Guardia, Isla de Margarita; El Rancho de Salvadore, S of Isla La Vaquita; Punta Mosquito (all RCB, *ex* C. Franz). BERMUDA: (numerous records). BAHAMA ISLANDS: (numerous records). GREATER ANTILLES: (numerous records). LESSER ANTILLES: (numerous records). BARBADOS: (numerous records); Bathsheba (ANSP, MCZ, USNM); S side of Ragged Point (ANSP); Hastings Rocks (BMNH). TRINIDAD: (MCZ; MNHNP; RCB, *ex* Bacon; USNM); Gulf of Paria (BMNH); Monos Id. (ANSP); Toco; rocks, W of Bath, Maguaripe Bay (both MCZ). CARIBBEAN ISLANDS: *Grand Cayman Id.*: S of Chapel, West Bay (ANSP); E end (DMNH); Gun Bay reef (ANSP, DMNH); *Cayman Brac*: (BMNH); Southwest Point (ANSP); *Curaçao*: (MCZ); San Juan (RCB); Westpuntbaai; Boca Porto Marie (both ZMA); S coast of Curaçao; St. Michaelsbaai (both RNHL); Spaansebaai (ZMA); Spaanse Put (RCB); *Bonaire*: Kralendijk (KMA); *Isla Orchila*: (USNM); *La Blanquilla*: Cabecera (RCB, *ex* C. Franz).

Chiton (*Chiton*) *stokesii* Broderip, 1832

(Figures 7–10, 12–17, 36, 39–43, 47, 48, 51)

Chiton stokesii Broderip [*in* BRODERIP & SOWERBY], 1832:25 (Port St. Elena, west coast of Colombia [Ecuador] and Panama; syntypes in BMNH); REEVE, 1847:pl. 1, sp. 4a, b; C. B. ADAMS, 1852:467; DALL, 1879:79, 126, pl. 3, fig. 24 [radula]; PILSBRY, 1893:165, pl. 30, figs. 25, 26, pl. 32, figs. 50–53; DALL, 1909:247; KEEN, 1958: 517, fig. 3; Thorpe [*in* KEEN], 1971:864, fig. 5; ABBOTT, 1974:405.

Chiton patulus SOWERBY, 1840a:fig. 134 (locality not given; location of type unknown); SOWERBY, 1840b:291; REEVE, 1847:pl. 6, sp. 30.

Lophyrus stokesii (Broderip). CARPENTER, 1857a:317.

Chiton interruptus Carpenter MS, *fide* PILSBRY, 1893:166.

Chiton (*Lophyrus*) *patulus* Sowerby. CLESSIN, 1903:5, fig. 1.

Chiton (*Lophyrus*) *stokesii* Broderip. CLESSIN, 1903:11, pl. 7, fig. 1.

Chiton stokesi [*sic*], var. *broderipi* CLESSIN, 1904:118, pl. 41, fig. 7 ([St. Elena] Westcolumbien [Ecuador]; reference to REEVE [1847:pl. 1, fig. 4b]; type in BMNH). *Non* Potiez & Michaud, 1838.

Chiton stokesi [*sic*] Broderip. BERGENHAYN, 1930:29, pl. 7, fig. 66; pl. 8, fig. 71; PILSBRY & LOWE, 1932:130; ABBOTT, 1954:326; LELOUP, 1956:54; KAAS & VAN BELLE, 1980: 124.

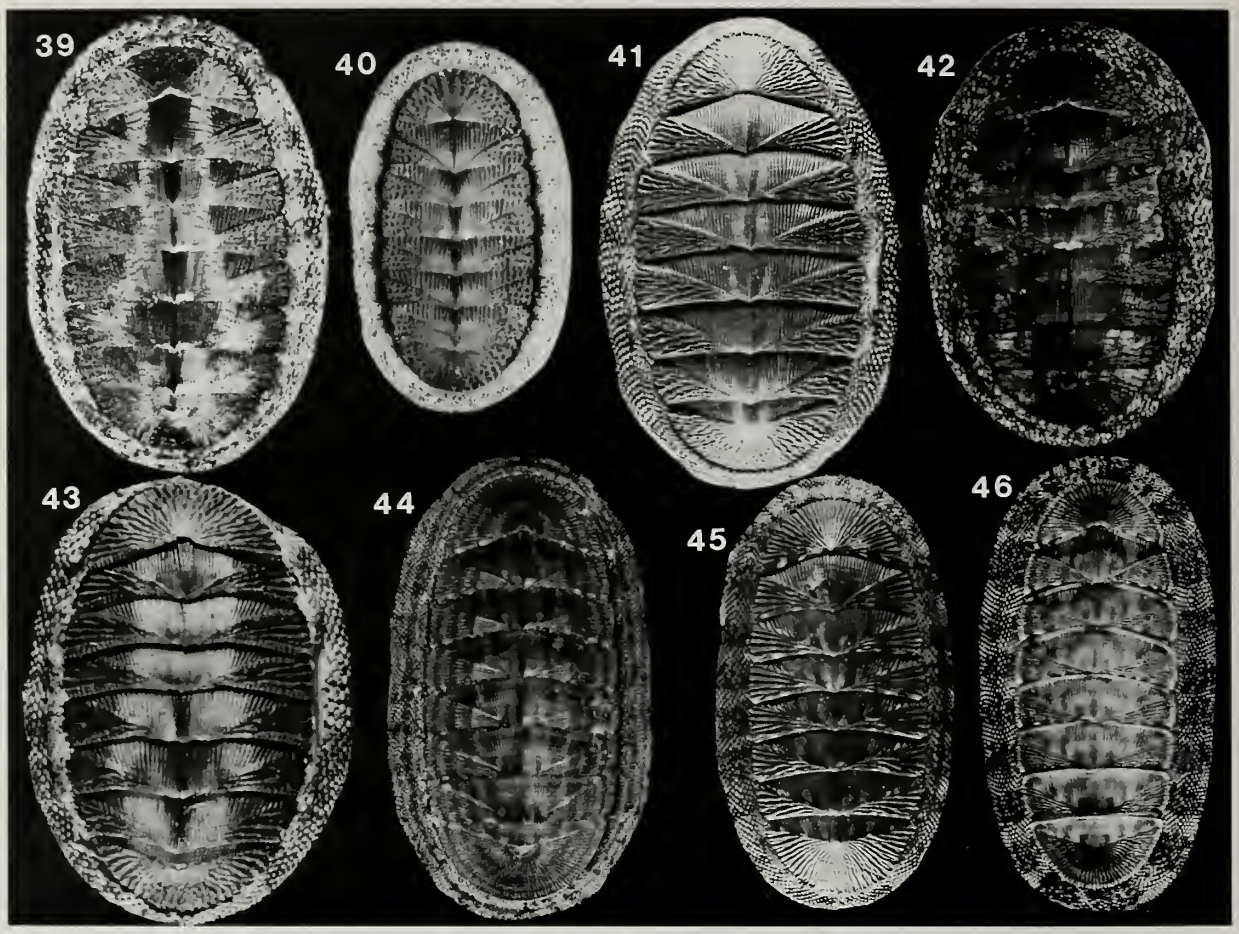
Chiton (*Chiton*) latus "Sowerby" BOONE, 1933:200, pl. 125, fig. B [reported from Galápagos Ids.; =*C. magnificus* Deshayes]. *Non* Sowerby, 1825.

Chiton (*Chiton*) *stokesii* Broderip. EMERSON & OLD, 1964: 92.

Chiton stockesii [*sic*] Broderip. CRUZ & SOTELA, 1984:61–68 [ecology, reproduction].

Non Chondroplax stockesi [*sic*] "Broderip" THIELE, 1893:364 [=*Chiton granosus* Frembly, *fide* THIELE, 1909].

Description: Animal reaching 90 mm in length, 60 mm in width. Angle of valves about 110°. Anterior valve slightly convex; post-mucronal region of posterior valve straight. Mucro rather blunt, anteriorly acentric on posterior valve. Jugal and central regions with numerous longitudinal ribs. Lateral triangle not raised, with seven irregular, radiating,



Explanation of Figures 39 to 46

Shells of *Chiton stokesii* Broderip and *C. virgulatus* Sowerby.

Figure 39. *Chiton stokesii,* Perico Id., Panama (RCB) (37 mm).

Figure 40. *C. stokesii,* Punta Mala, Panama (RCB) (21 mm).

Figure 41. **Syntype** of *Chiton stokesii* Broderip, St. Elena, West Colombia [Ecuador] (BMNH) (64.5 mm).

Figure 42. *C. stokesii,* N side of Isla Bona, Gulf of Panama (RCB) (29.5 mm).

Figure 43. **Holotype** of *Chiton stokesii,* var. *broderipi* Clessin [=*C. stokesii* Broderip], St. Elena, West Colombia [Ecuador] (BMNH).

Figure 44. *Chiton virgulatus,* Bahía Kino, Sonora, Mexico (MCZ 193026) (60 mm).

Figure 45. *C. virgulatus,* locality unknown (BMNH).

Figure 46. *C. virgulatus,* Puertecitos, Baja California (SDSC) (56 mm).

occasionally anastomosing ribs. End valves with numerous irregular, radiating, anastomosing ribs. Shell color dark brown, occasionally reddish, with a few white streaks on central areas. Girdle alternately banded light and dark. Interior of shell bluish white, apophyses white, insertion teeth mauve; posterior depression with reddish brown streaks.

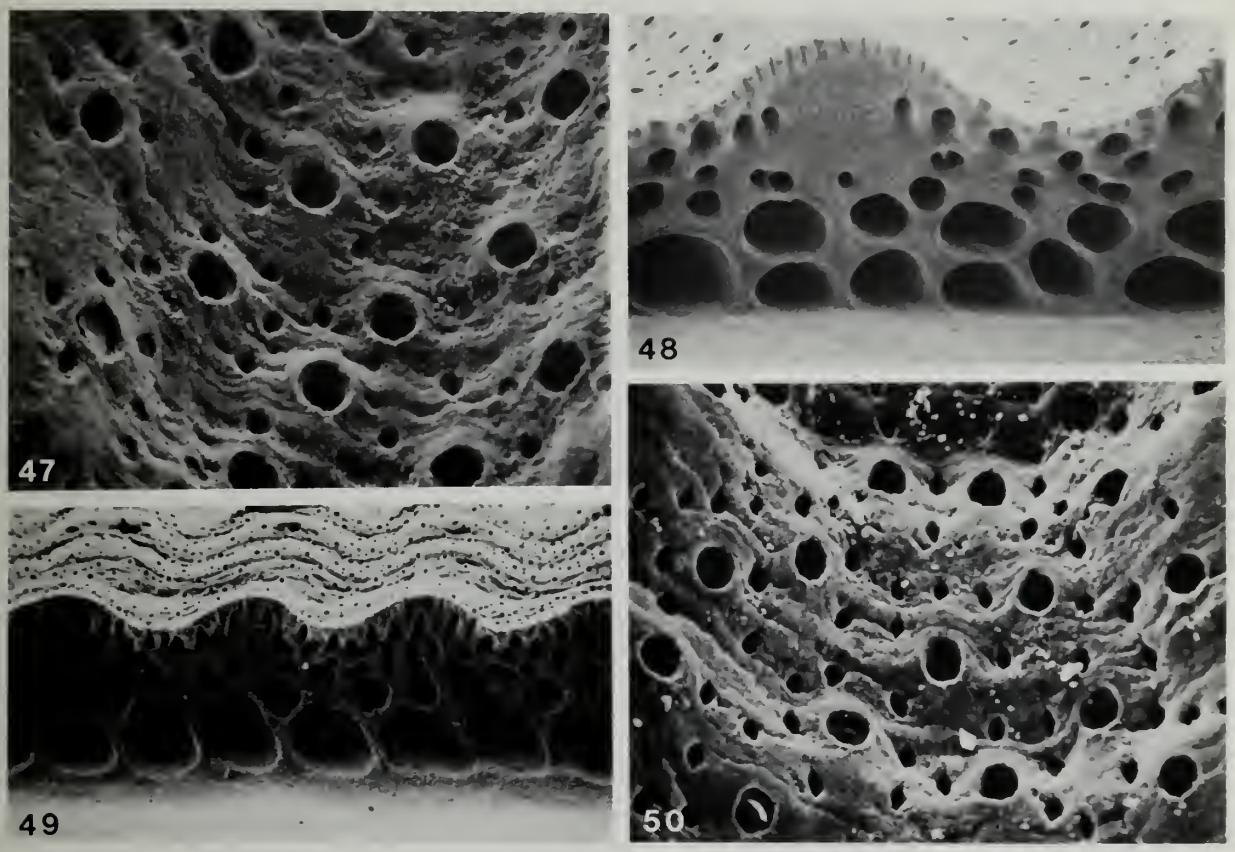
Tegmentum: Suprategmentum dark in color; subtegmentum with two or three rows of close-packed, moderate-sized canals, which are continuous over jugum (Figure 48).

Esthete pores: Megalopores with slightly beveled edges, three to four times as large as micropores. Megalopores often forming a volcano-like structure; the rather round to ovate and slitlike micropores lack this cone (Figure 47).

Articulamentum: Central depression of intermediate valves smooth. Primary slit-ray absent in adult specimens. Secondary slit-ray present laterally. Slit formula 17/1–2/16.

Girdle scales: Moderate in size, roundly triangular. Ventro-lateral sculpture of rather fine, sometimes anastomosing, longitudinal ribs which develop into a reticular pattern midway toward apex. Many small apical pustules evident; apical shelf present. Base slightly concave laterally, but lacking distinct basal compression (Figures 7–10).

Radula: Central tooth broad, evenly rounded distally, tapering basally. Pad of centro-lateral tooth conspicuously extended, constricted at point of attachment; a smaller pad is evident medially at end of scraping edge. Wing of major lateral elongate, bluntly pointed distally. Denticle cap rather



Explanation of Figures 47 to 50

Esthete pores and anterior tegmental innervation in *Chiton stokesii* Broderip and *C. virgulatus* Sowerby.

Figures 47 and 48. *Chiton stokesii,* Punta Mala, Panama (RCB) (Figure 47, ×376; Figure 48, ×94).

Figures 49 and 50. *C. virgulatus,* Bahía Kino, Mexico (MCZ 193026) (Figure 49, ×47; Figure 50, ×376).

attenuate, black tab elongate; magnetite not enclosing tab (Figures 12–17, 36).

Remarks: *Chiton stokesii* resembles the allopatric *C. virgulatus* Sowerby and, in fact, the two species probably share a relatively recent common ancestor. The esthete pores of the two species are virtually identical, and the volcano-like structure surrounding many of the megalopores (Figures 47, 50) serves to distinguish these two species from all other species of *Chiton.* The radulae of these two eastern Pacific chitons are quite similar; however, the girdle scales exhibit significant differences (compare Figures 7 and 32). *Chiton stokesii* differs from *C. virgulatus* by being less elongate; having a brown, not green, coloration; possessing larger girdle scales; and having a checkered pattern of radial sculpture on the lateral triangle. The subtegmentum of *C. stokesii* is not as well developed (Figure 48); it is highly developed in *C. virgulatus,* with large, conspicuous, close-packed canals (Figure 49).

Because older collections of Panamanian shells often include eastern Pacific as well as western Atlantic material, there has been some confusion between the Panamic *Chiton stokesii* and the West Indian *C. tuberculatus,* both of which occur commonly in Panama. *Chiton stokesii* is easily differentiated by having more numerous, straight, longitudinal ribs on the central area and jugum. In *C. tuberculatus* the jugum is smooth and the central area ribs are larger and curve medially as they proceed anteriorly (see remarks under *C. tuberculatus* for variation in southern Caribbean populations). In addition, the subtegmentum of *C. tuberculatus* is much more highly developed (Figure 28). The radulae differ considerably (compare denticle caps, Figures 35, 36).

The systematic position of *Chiton stokesii* is unclear. Characters of the tegmentum, such as the poorly developed subtegmentum, and the numerous ribs of the central area and jugum, point towards a *Radsia* placement. Other characters, however, are typically *Chiton,* such as the primary slit-ray and jugal tract which, unique among the Chitoninae, becomes obsolete in adult individuals. It is ironic that *C. stokesii* was erroneously included by THIELE (1893) in his new genus-group *Chondroplax,* because the radula of *Chiton stokesii* does have many similarities with *Chiton* (*Chondroplax*) *granosus,* but THIELE (1909) noted that his

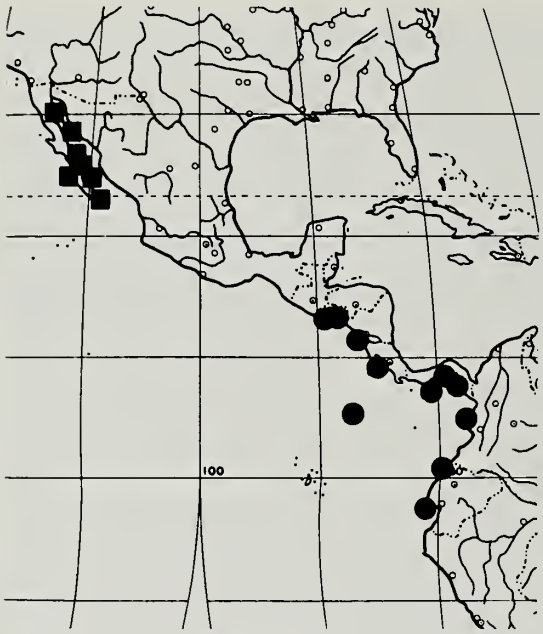


Figure 51

Distribution of *Chiton stokesii* Broderip (●) and *C. virgulatus* Sowerby (■).

earlier identification was in error. The shells of these two species are quite different.

The tegmentum of *Chiton stokesii* is normally dark brown with a few light jugal streaks, but may be much lighter; some specimens are nearly white. Many examples from Panama reveal that the valves of young specimens may be partially or totally white (Figures 39, 40, 42). A few reddish brown individuals were observed from Panamanian and Colombian localities (cf. REEVE [1847:pl. 1, sp. 4b, var. β]). This change in pigmentation is not common. Various dark-colored chitons have been noted to have a red portion on one valve (all in the same growth zone) or, in the case of *C. stokesii,* in the entire shell.

Little is known concerning the biology of *Chiton stokesii.* Along the Pacific coast of Panama, *C. stokesii* is the only large chiton found, and it utilizes the entire intertidal zone, younger individuals as a rule being found lower in the intertidal zone than adults. This situation sharply contrasts with the spatial distribution of the various Caribbean species where the sympatric *Chiton* species are vertically zoned (GLYNN, 1970). In the Bay of Panama, *C. stokesii* is found during the day under rocks and in the numerous crevices along the rocky shores. CRUZ & SOTELA (1984) reported on the biology of *C. stokesii* in Costa Rica. They noted densities as high as 6.3/m^2 in the lower intertidal zone and that *C. stokesii* has more than a single spawning season.

The presence of the bivalve *Lithophaga aristata* (Dillwyn) as an endosymbiont of *Chiton stokesii* was reported by BULLOCK & BOSS (1971) who noted that the degree of infestation can be very great. The use of the term "parasite" in this case is questionable as the relationship between host and "parasite" does not appear to be obligatory. *Lithophaga,* which normally bores into hard, calcareous substrate such as limestone, coral slabs, and large shells, was found to bore into the articulamentum and the more organic matrix of the tegmentum which contains the esthete system. The consequence of *Lithophaga* infestation of chiton valves is not known. In a similar case, an endolithic acrothoracic barnacle was reported within the valves of *Sypharochiton pelliserpentis,* and was suggested to affect the behavior of the host (Johns *in* KNOX, 1963).

Various authors have "corrected" the "*-ii*" ending of *Chiton stokesii* to "*-i,*" believing that "*i*" and "*ii*" are the same and that the former is the correct patronymic ending. While "*-i*" and "*-ii*" are the same with regard to homonymy (ICZN Art. 58(12), the "*-ii*" ending must be used in this case because it is the correct original spelling (ICZN Art. 33d).

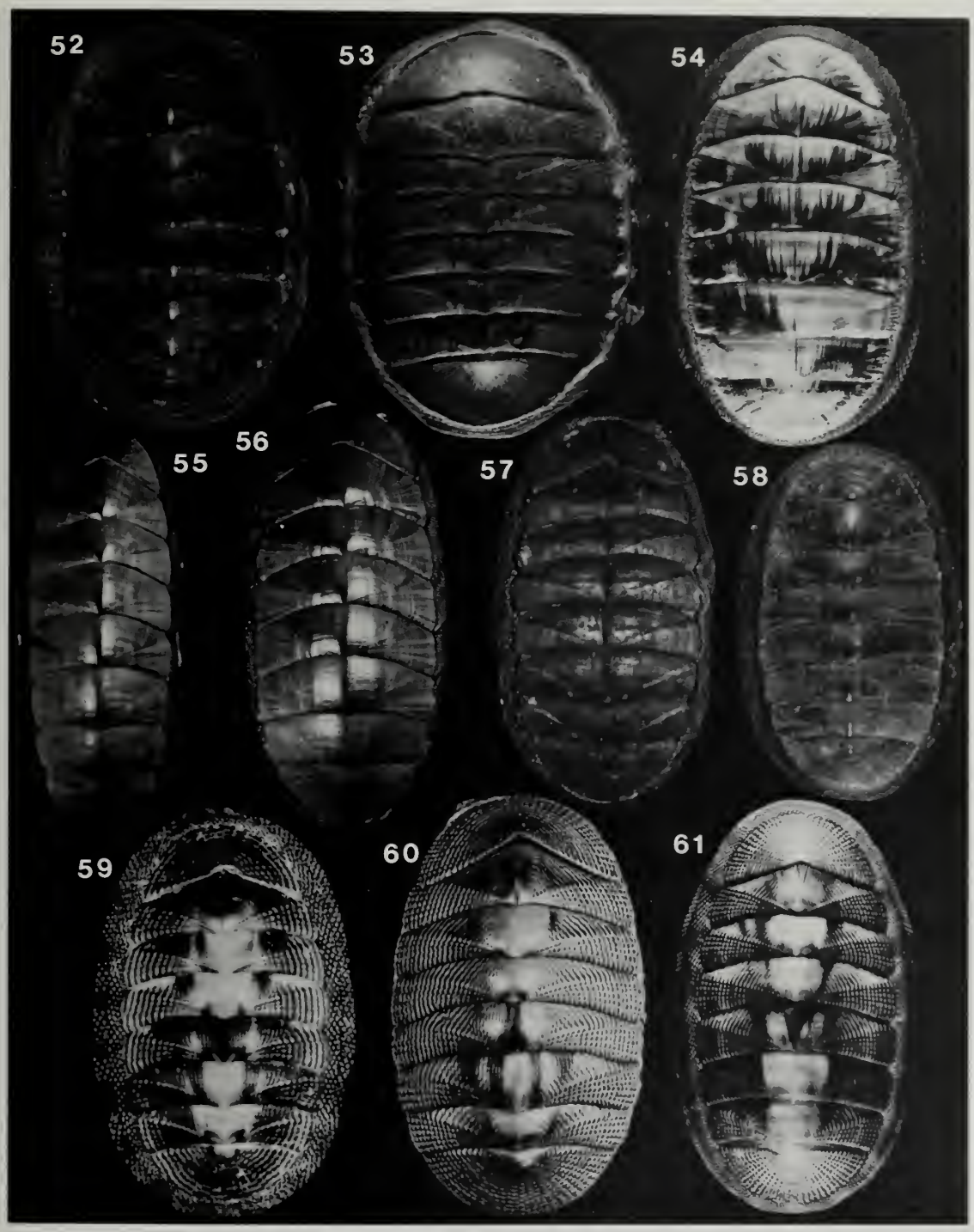
Distribution: *Chiton stokesii* occurs from Guatemala south to Ecuador (Figure 51). The species also occurs on Cocos Island, but its presence on the Galápagos Islands (BOONE, 1933: as *C. latus* Sowerby) needs confirmation. SMITH & FERREIRA (1977) did not record this species from the Galápagos Islands. DALL (1909) gave the range of *C. stokesii* as "Guaymas, Mexico, south to Arica, Chile"; this inaccurate statement probably resulted from confusion with the northern *C. virgulatus* and from erroneous museum labels.

Locality records: GUATEMALA: (USNM). EL SALVADOR: San Salvador (USNM). HONDURAS: Golfo de Fonseca (ZMK). NICARAGUA: (ANSP); Corinto (ANSP); San Juan del Sur (ANSP, MCZ, USNM, ZMK). COSTA RICA: Playas del Coco [10°31'N, 85°43'W] (RCB, *ex* Spight); Puntarenas (ZMK); mouth of Rio Barranca, near Puntarenas (ANSP). PANAMA: Punta Mala; Playas El Uverito, just N of Puerto Mensabé, Las Tablas (both RCB); Morro de Puercos (USNM); Bay of Panama (MNHNP, USNM); Isla Venado (ANSP); Naos Id.; Perico Id.; Flamenco Id. (all RCB); W of Panama City (ANSP); Panama City (numerous records); Isla Taboguilla (USNM); Isla Taboga (ANSP, MCZ, USNM, ZMK); Morro de Taboga; between Morro de Taboga and Isla Taboga; Hotel Taboga, NE Isla Taboga (all ANSP); W side, Isla Taboga (RCB); E side of Isla Bartolomé, Archipiélago de las Perlas (MCZ); Isla San José, Archipiélago de las Perlas (USNM); Isla Senora y Isla Senorita (MCZ). COLOMBIA: Choco Prov. (ANSP). ECUADOR: (ANSP, BMNH, MNHNP); Punta Carnero (BMNH); San Lorenzo (USNM); Santa Elena; Punta Santa Elena (both ZMK); Salinas; off Playas (both USNM); Puná (NRS). OFFSHORE IDS.: *Cocos Island*: (ANSP, BMNH, MCZ, USNM); Chatham Bay (ANSP, DMNH, MCZ); Wafer Bay (ANSP).

Chiton (*Chiton*) *virgulatus* Sowerby, 1840

(Figures 32, 37, 44–46, 49, 50, 51)

Chiton virgulatus SOWERBY, 1840a:fig. 132 (locality unknown [herein designated to be Bahía Kino, Sonora, Mexico];



Explanation of Figures 52 to 61

Shells of New World *Chiton* (*Amaurochiton*).

Figure 52. *Chiton magnificus magnificus* Deshayes, locality unknown (RCB) (79 mm).

Figure 53. *C. magnificus magnificus,* Valparaiso, Chile (MCZ 204314) (40 mm).

Figure 54. *C. magnificus,* Chile (BMNH) (68 mm).

Figures 55 and 56. **Syntypes** of *Chiton bowenii* King [=*C. magnificus bowenii*], Terra del Fuego (BMNH) (Figure 55, 73.5 mm; Figure 56, 55 mm).

Figures 57 and 58. Probable **Syntypes** of *Chiton subfuscus* Sowerby [=*C. magnificus magnificus* × *C. magnificus bowenii*], Isla de Chiloé, Chile (ZMK, *ex* Cuming) (Figure 57, 52 mm; Figure 58, 38 mm).

Figure 59. *Chiton cumingsii* Frembly, locality unknown (26 mm) (RCB).

Figure 60. *C. cumingsii,* Talcahuano, Chile (MCZ) (43 mm).

Figure 61. *C. cumingsii,* Valparaiso, Chile (BMNH) (51 mm).

location of type unknown); SOWERBY, 1840b:291; REEVE, 1847:pl. 21, sp. 140; PILSBRY, 1893:166, pl. 32, figs. 54–56; PILSBRY & LOWE, 1932:130; ABBOTT, 1954:325; KEEN, 1958:518, fig. 5; Thorpe [*in* KEEN], 1971:405, fig. 4751; KAAS & VAN BELLE, 1980:141.

Chiton (*Lophyrus*) *virgulatus* Sowerby. CLESSIN, 1903:55, pl. 20, fig. 5.

Description: Animal reaching 62 mm in length and 35 mm in width. Angle of valves about 110°. Anterior valve and post-mucronal slope of posterior valve convex. Mucro blunt, anteriorly acentric on posterior valve. Jugal and central regions with about 36 rounded ribs per side. Lateral triangle raised, with 13–16 irregular, radiating ribs which occasionally bifurcate. End valves with numerous irregular radial ribs. Shell color olive green with a few longitudinal streaks of black on each side, concentric stripes on terminal areas, and occasional lighter spots throughout. Girdle light grayish green with scattered darker scales and usually some evidence of banding. Interior of shell light blue.

Tegmentum: Suprategmental layer thin; subtegmentum well developed, composed ventrally of a row of large, close-packed canals; above these holes is a row of medium-sized canals with occasional smaller canals above (Figure 49).

Esthete pores: Megalopores large, rounded with slightly beveled edges, three to four times as large as the micropores, and forming a volcano-like structure. The ovate, slitlike micropores lack this cone (Fig. 50).

Articulamentum: Central depression of intermediate valves with a number of thin grooves that extend beyond confines of jugal tract; slits present within these grooves in jugal tract. Jugal slits extend posteriorly over callus, become more prominent, and reach mucronal callus. Primary and secondary slit-rays well developed, with highly irregular, elongate slits, one per longitudinal row. Slit formula 18/1–2/18.

Girdle scales: Medium in size, dorsally rounded. Ventrolateral areas with fine, at times granular longitudinal ribs. Rest of scale smooth except for some low, broad nodules toward apex (Figure 32).

Radula: Central tooth rather wide, deeply concave distally, tapering to half the width basally. Centro-lateral tooth with ovate pad laterally, and a thickening distally on medial edge. Wing of major lateral tooth quite flat, very extended, somewhat pointed. Denticle cap elongate, pointed, with moderately extended black tab distally, magnetite on back surrounds the tab; a tan area (probably lepidocrocite) appears only laterally (Figure 37).

Remarks: *Chiton virgulatus* is closely related to *C. stokesii,* but differs by its usually more elongate shape, greener coloration, relatively smaller girdle scales, and finer radial ribs on the terminal areas. In *C. stokesii* the radial sculpture of the terminal areas nearly always forms a checkered pattern, giving the valve a granulated appearance. In addition, the subtegmentum in *C. virgulatus* is very well developed with large, close-packed canals (Figure 49); in *C. stokesii* the subtegmentum is not well developed, the canals are smaller and not as close-packed (Figure 48). The esthete pore pattern is nearly identical in the two species (Figures 47, 50).

Chiton virgulatus is easily distinguished from its sympatric congeners, *C.* (*Diochiton*) *albolineatus* and *C.* (*Diochiton*) *articulatus* by having the central area ribbed rather than smooth.

Distribution: *Chiton virgulatus* is restricted to Baja California and the Gulf of California region (Figure 51). Published records suggest that *C. virgulatus* and *C. stokesii* are sympatric over parts of their ranges. ABBOTT (1974), for example, recorded the range of *C. virgulatus* as Baja California to Panama, and *C. stokesii* as Mexico to Colombia. A critical examination of specimens with precise locality data has revealed no evidence for sympatry in these two closely related species. Thorpe (*in* KEEN, 1971) reached a similar conclusion.

Locality records: MEXICO: Bahía Magdalena (ANSP); Gulf of California (MCZ); Ensenada de los Muertos (USNM); La Paz (USNM, ANSP); S side of Bahía Pichilinque; Punta Prieta; Isla Espíritu Santo; Isla Partida; Isla San José; Bahía Agua Verde; Puerto Escondido, Bahía de Las Animas; Bahía San Francisquito; Isla Angel de la Guarda, Puerto Refugio (all USNM); Puertecitos (SDSC); San Felipe (ANSP, DMNH, MCZ, MNHNP, USNM); Bahía Kino (MCZ).

Chiton (*Chiton*) *sulcatus* Wood, 1815

(Figures 25, 26, 29, 30, 33, 34, 38)

Chiton sulcatus WOOD, 1815:16, pl. 3, fig. 1 (South Seas [herein restricted to Isla San Salvador (=James Island), Galápagos Islands]; type presumed lost); WOOD, 1825: 3, pl. 1, fig. 20; REEVE, 1847:pl. 3, sp. 15; STEARNS, 1893:404; BERGENHAYN, 1930:29, pl. 8, figs. 70, 73 [shell structure]; Thorpe [*in* KEEN], 1971:864, fig. 6; SABELLI & TOMMASINI, 1980:405. *Non* Risso, 1826, *non* Quoy & Gaimard, 1835.

Lophyrus sulcatus (Wood). CARPENTER, 1857a:360.

Chiton (*Radsia*) *sulcatus* Wood. PILSBRY, 1893:191, pl. 28, figs. 1–4; STEARNS, 1893:449; DAUTZENBERG & BOUGE, 1933:419 [erroneously reported from Marutea du Sud (Tuamotu Ids.)]; BOONE, 1933:202, pl. 127; SMITH & FERREIRA, 1977:89, fig. 14 [reported from the Pleistocene, Galápagos Ids.]; KAAS & VAN BELLE, 1980:128.

Chiton woodii CLESSIN, 1903:49, pl. 18, fig. 1 [unnecessary new name for *Chiton sulcatus* Wood, 1815].

Description: Animal reaching 95 mm in length and 53 mm in width. Angle of valves about 115°. Anterior valve convex; post-mucronal slope of posterior valve straight. Mucro blunt, anteriorly acentric on posterior valve. Jugal and central regions with 12–15 squarish, longitudinal ribs per side. Lateral triangle with two to three large, irregular ribs, which may bifurcate to form secondary ribs. Terminal areas with 16–20 prominent ribs, nearly all dividing to form a second rib. Shell color dark greenish black, occasionally reddish brown. Girdle black. Interior of valves light bluish white with reddish brown in central and posterior depressions.

Tegmentum: Suprategmentum reduced; subtegmentum composed ventrally of large, close-packed canals with smaller canals restricted to the area above each longitudinal rib. Subtegmentum present over jugum (Figure 29).

Esthete pores: Megalopores large, round, with beveled edges, about twice as wide as the round to ovate micropores which seem less ordered than in most other species of *Chiton s.s.* (Figure 30).

Articulamentum: Central depression of intermediate valves with numerous transverse grooves; these grooves with occasional slits within jugal tract. A band of circular to oval slits extends from callus to mucronal callus in jugal region of posterior depression. Primary and secondary slit-rays present, one slit per row. Slit formula 20/2–3/21.

Girdle scales: Large, rounded. Sculpture of fine (sometimes anastomosing) longitudinal ribs ventro-laterally and reticular ribbing distally. Apical pustules very small. Apical shelf narrow (Figure 33).

Radula: Central tooth rather broad, cupped distally, and tapering basally. Centro-lateral pad small. Denticle cap elongate, pointed, with extended black tab; magnetite not enclosing the tab. Wing of major lateral tooth elongate, pointed distally (Figure 34).

Remarks: *Chiton sulcatus* has the boldest sculpture of any *Chiton* known and does not appear to be very closely related to any other Recent *Chiton,* although it has some similarity to the West Indian *C. tuberculatus* Linnaeus (see remarks under that species). *Chiton sulcatus,* however, does show a strong resemblance to *Chiton* (*Chiton*) *rossi* Smith *et al.,* 1968, described from the Upper Cretaceous of Puerto Rico. *Chiton sulcatus* has multiple slits in the insertion plate of the intermediate valve, a characteristic of a number of Panamic *Chiton,* while *C. rossi* exhibits a single slit per side. *Chiton goodallii* Broderip, the only other large chiton endemic to the Galápagos Islands, differs in being smooth.

Smith & Ferreira (1977) considered Wood's (1815) type locality of *Chiton sulcatus* "South Seas" too general, and stated: "Isla San Salvador (James Island) may be accepted as the type locality for *Chiton sulcatus* based on Reeve's first localized island record." Such a statement cannot be accepted as a valid designation of the type locality because of the words "may be accepted as" and the fact that mere mention of a specific locality does not constitute a type locality designation (ICZN, recommendation 72E). In order to clarify this situation, the type locality of *Chiton sulcatus* Wood is herein restricted to Isla San Salvador [=James Island], Galápagos Islands.

Distribution: *Chiton sulcatus* is known only from the Galápagos Islands (Figure 38). The few records from Peru have not been confirmed by reliable collections. The published report that this species occurs in the Tuamotu Islands (Dautzenberg & Bouge, 1933) is certainly in error.

Locality records: Galápagos Islands: *Isla San Cristobal* [Chatham Id.]: (MCZ); Wreck Bay (ANSP, DMNH, MCZ). *Isla Española* [Hood Id.]: (ANSP, BMNH, MNHNP, USNM, ZMHU); Gardner Bay; Gardner Id. (both ANSP). *Isla Santa Maria* [Charles Id.]: (MCZ, ZMK); Black Beach (ANSP). *Isla Santa Cruz* [Indefatigable Id.]: Darwin Station (ANSP); Seymour Bay (ANSP, MCZ); on rocks, extreme low tide at night, Academy Bay (USNM). *Isla Isabela* [Albemarle Id.]: (MCZ); Tagus Cove (ANSP, USNM); Elizabeth Bay (USNM). *Isla Fernandina* [Narborough Id.]: (BMNH); opposite Tagus Cove (ANSP, MCZ).

Subgenus *Amaurochiton* Thiele, 1893

Amaurochiton Thiele, 1893:362. Type species by subsequent designation of Iredale & Hull (1926), *Chiton olivaceus* Frembly, 1827 [=*Chiton magnificus* Deshayes, 1827], *non C. olivaceus* Spengler, 1797.

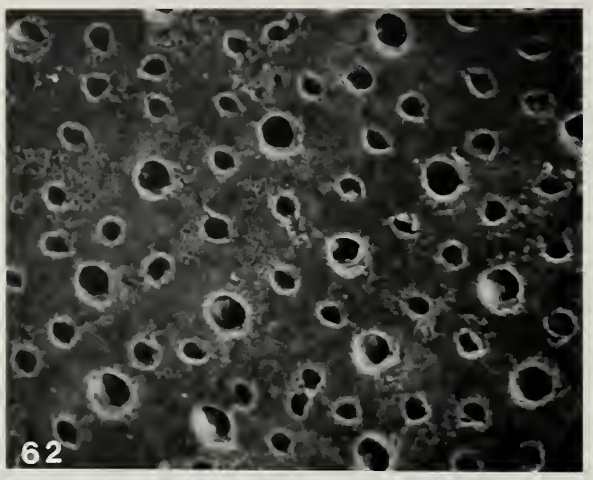
Poeciloplax Thiele, 1893:365. Type species by monotypy, *Poeciloplax glauca* [Gray] [=*Chiton glaucus* Gray, 1828].

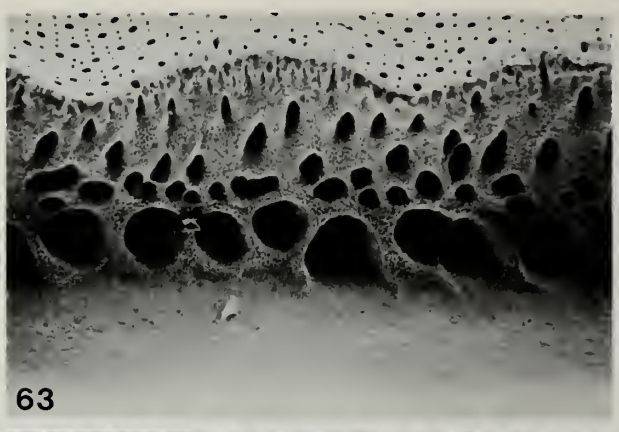
Description: Animal reaching 90 mm in length and 55 mm in width. Central and jugal areas with low, smooth, longitudinal ribs, rarely smooth. Lateral triangle and terminal areas with broad and slightly nodular, or fine, radial ribs. Subtegmentum moderately to highly developed. Girdle scales medium to fairly large, smooth except for fine longitudinal striations laterally near base; ventro-lateral reticular sculpture in one case.

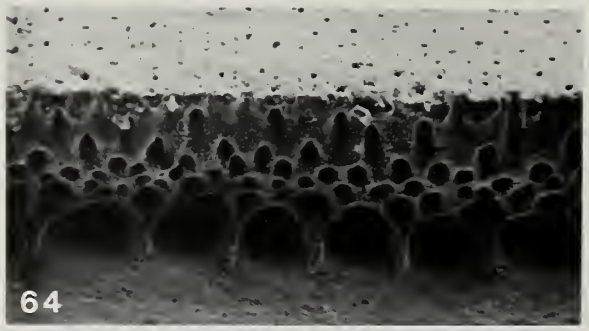
Remarks: When Thiele (1893) established this genus-group name, the included species were: *Amaurochiton olivaceus* (Frembly), *A. cumingi* [*sic*] (Frembly), *A. striatus* (Barnes), and *A. tenuistriatus* (Sowerby). However, Thiele (1909:2) corrected his earlier misidentifications, reporting that he had actually been working with *Chiton magnificus* Deshayes, *C. cumingsii* Frembly, *C. subfuscus* Sowerby, and *C. subfuscus* Sowerby, respectively. Furthermore, Thiele (1909) did not recognize any taxonomic value of his name *Amaurochiton.* Iredale & Hull (1926) stated that the type species of *Amaurochiton* was *Chiton olivaceus* Frembly [=*C. magnificus* Deshayes] by monotypy. Although this type designation cannot be "by monotypy" because *Chiton cumingsii* Frembly was also included in the original description, this type designation is valid according to ICZN Art. 69a(iv).

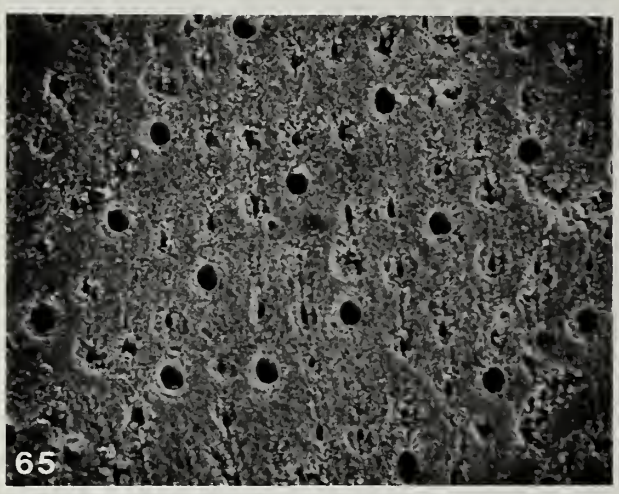
The taxonomic use of the name *Amaurochiton* has been inconsistent. Australians, notably Iredale (1914, 1915), Iredale & Hull (1926, 1927, 1932), and Allan (1959), accorded it full generic rank, in spite of the fact that Thiele himself (1909) had rejected the name. In the *Handbuch der Systematischen Weichtierkunde,* Thiele (1929) utilized *Amaurochiton,* but only as a section of *Chiton s.s.* More recently, Leloup (1956), Van Belle (1978, 1983) and Kaas & Van Belle (1980) treated *Amaurochiton* as a synonym of *Chiton. Amaurochiton* is used in the present report to denote a lineage of southern hemisphere *Chiton.*

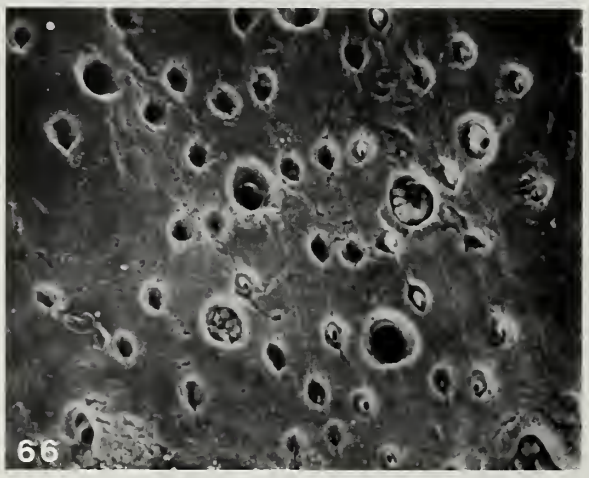
Amaurochiton differs from *Chiton s.s.* by the numerous, generally smooth, longitudinal ribs on the jugal and central areas and the smooth radial ribs of the lateral triangle and

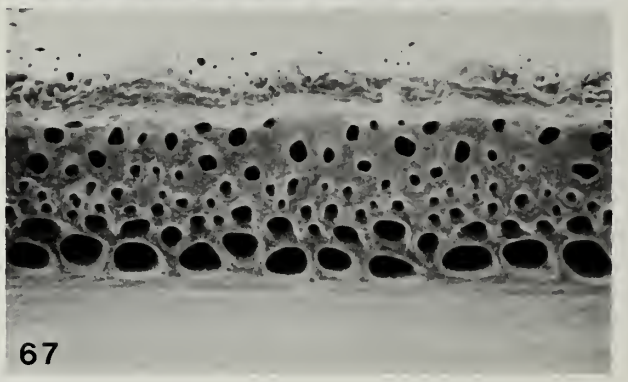












Explanation of Figures 62 to 67

Esthete pores and anterior tegmental innervation of *Chiton* (*Amaurochiton*).

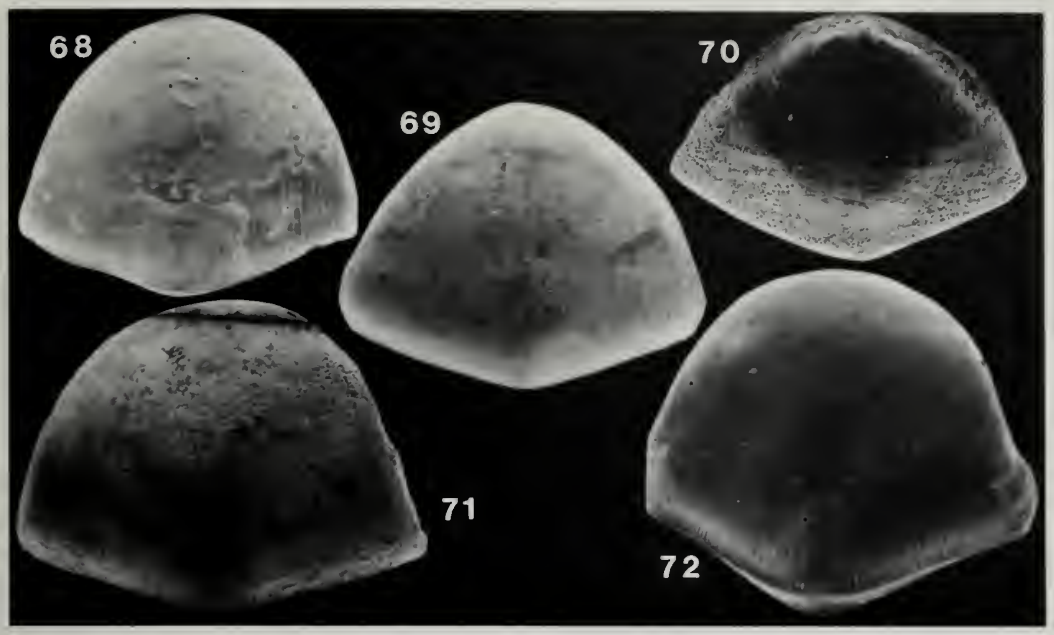
Figures 62 and 63. *Chiton cumingsii* Frembly, Talcahuano, Chile (MCZ) (Figure 62, ×336; Figure 63, ×84).

Figures 64 and 65. *Chiton subfuscus* Sowerby [=*C. magnificus magnificus* × *C. magnificus bowenii*], Isla de Chiloé, Chile (ZMK) (Figure 64, ×84; Figure 65, ×336).

Figures 66 and 67. *Chiton glaucus* Gray, Oriental Bay, Wellington, New Zealand (MCZ 277777) (Figure 66, ×336; Figure 67, ×84).

terminal areas; in *Chiton s.s.* the longitudinal ribs are not usually smooth and the ribs of the lateral triangle bifurcate and they are often nodular. Also, the rather smooth girdle scales separate *Amaurochiton* from *Chiton s.s.*, although *C. glaucus*, which is herein included in *Amaurochiton*, differs in this respect by having fine reticular ventro-lateral sculpture that is seen in *Chiton s.s.*

The three members of *Amaurochiton* are restricted to the southern hemisphere. Included species are: *Chiton cumingsii* and the polytypic *C. magnificus* from the eastern coast



Explanation of Figures 68 to 72

Girdle scales of *Chiton* (*Amaurochiton*).

Figure 68. *Chiton subfuscus* Sowerby [=*C. magnificus magnificus* × *C. magnificus bowenii*], Isla de Chiloé, Chile (ZMK) (×65).

Figure 69. *C. cumingsii* Frembly, Valparaiso, Chile (BMNH) (×163).

Figure 70. *C. glaucus* Gray, Oriental Bay, Wellington, New Zealand (MCZ 277777) (×62).

Figure 71. *C. magnificus bowenii,* locality unknown (BMNH) (×74).

Figure 72. *C. magnificus magnificus,* Chile (MCZ) (×45).

of South America, and *C. glaucus* from southeastern Australia and New Zealand.

KEY TO THE SPECIES OF THE SUBGENUS *Amaurochiton*

1. Color of lateral triangle cream white to greenish yellow with conspicuous longitudinal light brown lines which may be present only on nodules ..... *C. (A.) cumingsii*
   Color of lateral triangle variable, including solid colors, dark streaks, or small bluish white spots 2
2. Ribs of lateral triangle and central area greatly reduced or absent; girdle scales relatively small; valves sometimes very carinate; color black or red, occasionally streaked ... *C. (A.) magnificus bowenii*
   Ribs of lateral triangle and central area not reduced; girdle scales relatively large; valves broadly rounded or carinate; shell often unicolored 3
3. Valves moderately carinate; ribs of lateral triangle and central area very fine; shell color variable, usually unicolored; ventro-lateral areas of girdle scales with reticulate sculpture; denticle cap of major lateral tooth elongate, with black tab one-half length of cap ..... *C. (A.) glaucus*
   Valves broadly rounded; ribs of lateral triangle and central area relatively broad; shell color typically black with small scattered bluish white spots [some specimens may be ivory or orange-red with various black markings]; ventro-lateral areas of girdle scales with fine ribs; denticle cap of major lateral tooth squarish, with black tab that is one-fourth length of cap .. *C. (A.) magnificus magnificus*

Chiton (Amaurochiton) magnificus magnificus Deshayes, 1827

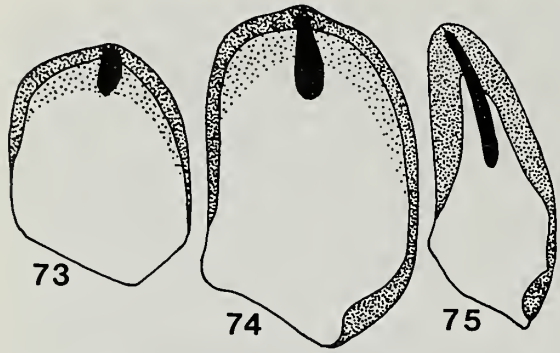
(Figures 52–54, 57, 58, 64, 65, 68, 72, 73, 76)

Chiton striatus BARNES, 1824:7:70, pl. 3, fig. 1 (coast of Peru; type presumed lost); SOWERBY, 1840a:3, figs. 3, 41; REEVE, 1847:pl. 1, sp. 3b; KAAS & VAN BELLE, 1980: 125. *Non* Fischer von Waldheim, 1807, *non* (Chiereghini) Nardo, 1847, *non* (Chiereghini) Brusina, 1870.

Chiton latus SOWERBY, 1825:appendix, p. v (locality unknown [herein designated to be Valparaiso, Chile]; location of type unknown); DALL, 1909:247; LELOUP, 1956:7, figs. 26, 27; OTAÍZA & SANTELICES, 1985:229–240 [vertical zonation]. *Non* Lowe, 1825.

Chiton olivaceus FREMBLY, 1827:199, pl. 16, fig. 4 (new name for *C. latus* Sowerby, 1825, *non* Lowe, 1825). *Non* Spengler, 1797.

Chiton magnificus DESHAYES, 1827:454 (les mers du Chili [herein restricted to Valparaiso]; location of type unknown); REEVE, 1847:pl. 1, sp. 3; PILSBRY, 1893:160, pl. 30, figs. 23, 24; NIERSTRASZ, 1905a:84, pl. 8, fig. 208; THIELE, 1909[in part]:2.



Explanation of Figures 73 to 75

Representative denticle caps of *Chiton* (*Amaurochiton*).

Figure 73. *Chiton magnificus magnificus* Deshayes, Chile (MCZ).

Figure 74. *C. cumingsii* Frembly, Talcahuano, Chile (MCZ).

Figure 75. *C. glaucus* Gray, Portobello, Otago Harbour, South Id., New Zealand (RCB, *ex* R. D. Turner).

Chiton subfuscus SOWERBY, 1832:26 (Island of Chiloé; location of type unknown); PILSBRY, 1893:162, pl. 38, figs. 19–22; PLATE, 1899:64 [anatomy]; DALL, 1909:247; THIELE, 1909:2; KAAS & VAN BELLE, 1980:127.

Chiton striatus, var. *subfuscus* Sowerby. SOWERBY, 1840a:3.

Chiton murrayi HADDON, 1886:21, pl. 1, fig. 7; pl. 3, figs. 7a–e (Valparaiso; type BMNH 89.11.9.14–15); PILSBRY, 1893:162, pl. 38, figs. 19–22.

Amaurochiton tenuistriatus "Sowerby" THIELE, 1893:363, pl. 30, fig. 7 [radula]. *Non Chiton tenuistriatus* Sowerby, *fide* THIELE (1909).

Amaurochiton olivaceus (Frembly). THIELE, 1893:362, pl. 30, fig. 4 [radula].

Amaurochiton striatus (Barnes). THIELE, 1893:363, pl. 30, fig. 6 [radula].

Chiton subfuscus, var. *mesoglyptus* PILSBRY, 1893:164, pl. 38, figs. 20–22 ([Chile]; type ANSP 35869).

Chiton (*Lophyrus*) *magnificus* Deshayes. CLESSIN, 1903:8, pl. 6, fig. 1.

Chiton (*Lophyrus*) *striatus* Barnes. CLESSIN, 1904:116, pl. 41, fig. 5.

Chiton (*Amaurochiton*) *magnificus* Deshayes. THIELE, 1929: 20, fig. 10.

Chiton latus Sowerby, form *subfuscus* Sowerby, 1832. LELOUP, 1956:51.

Description: Animal reaching 90 mm in length and 55 mm in width. Valves flattened to moderately carinate, angle 115–140°. Anterior valve slightly convex; post-mucronal slope concave. Mucro blunt, anteriorly acentric on posterior valve. Jugum and central areas with numerous longitudinal ribs, 41 per side, which may be faint or absent, except at the jugum. Lateral triangle barely raised, with eight to 12 low, radiating ribs. Shell color dark slate-gray, ivory, or orange-red; various black markings present; scattered light colored spots appear blue on dark specimens. Girdle black to brown. Interior of shell white.

Tegmentum: Suprategmentum thick, ventral layer with numerous small canals; subtegmentum composed of small to medium, close-packed canals (Figure 64).

Figure 76

Distribution of the *Chiton* (*Amaurochiton*) *magnificus* complex. *Chiton magnificus magnificus* Deshayes (■). *Chiton magnificus bowenii* King (●). Area of intergradation that includes both subspecies and intergrades between them (▲).

Esthete pores: Megalopores of medium size, round, about three to four times as large as the ovate micropores (Figure 65).

Articulamentum: Central depression of intermediate valves with scattered slits. Primary slit-ray with numerous close-packed slits, occasionally a few per row. Secondary slit-ray present laterally. Slit formula 11–14/1/14–19.

Girdle scales: Varying somewhat in size, medium to large, roundly triangular; ventro-lateral sculpture of thin, only slightly irregular striae which are hidden by overlapping scales. Naturally visible portions of the dorso-lateral surface smooth except for a few obscure nodules (Figures 68, 72).

Radula: Central tooth rather narrow, of even width along its length, somewhat cup-shaped distally. Pad of centro-lateral tooth elongate, irregular in appearance, and attached directly to tooth. Wing of major lateral paddle-shaped, rounded distally. Denticle cap shovel-like, squarish distally, tab ovate (Figure 73).

Remarks: *Chiton magnificus* differs from *C. cumingsii*, the only other eastern Pacific *Amaurochiton*, by its smoother sculpture and lack of the reddish brown lines on the lateral triangle and central area of the shell plates. The Australian–New Zealand *Chiton* (*Amaurochiton*) *glaucus* Gray differs from *C. magnificus* by having finer sculpture, a

unicolored shell and the reticular sculpture on the ventrolateral areas of the girdle scales. The radulae differ in the morphology of the denticle cap (Figures 73–75).

When *Chiton magnificus* is colored other than blue-gray, the characteristic blue spots are difficult to observe or even lacking; thus, they should not be used to characterize the species. *Chiton magnificus* is well represented in large collections, but most of the lots with locality data are from Valparaiso, Chile. For this reason, little can be said concerning intraspecific variation in this large Chilean chiton. The specimens from Valparaiso are rather uniform and numerous small blue spots on the shell-plates are easily visible. LELOUP (1956) considered the various names applied to this species and, in discussing intraspecific variation, he resorted to the infraspecific category of *forma*. With the exception of *C. bowenii* King, I concur with Leloup's synonymy. Some specimens from the Chiloé Province region, called *C. subfuscus* Sowerby, have less prominent sculpture, more elevated valves, and occasionally smaller scales (Figures 54, 57, 58). Individuals in this area include intergrades between typical *C. magnificus* and a southern subspecies, *C. magnificus bowenii*. A typical *C. m. bowenii* has little or no sculpture, highly arched valves, and very small scales (Figures 55, 56). The frequency of reddish individuals is much greater in *C. m. bowenii* than in the intermediate populations. Until many more specimens from a number of localities are available for study, I prefer to maintain *C. m. bowenii* at subspecific rank.

The nearly complete geographic isolation of the two subspecies of *Chiton magnificus* is evident, but an explanation of the evolution and maintenance of these two entities is presently lacking. It is interesting to note, however, that the known zone of intergradation for the subspecies is in the region of Isla de Chiloé. According to OLSSON (1961), a northern element of the West Wind Drift flows eastward and reaches the southern Chilean coast near Isla de Chiloé. One portion of this current then turns north and forms the Peruvian Current; the other portion flows south and goes around Cape Horn. The influence of these currents, as well as the winds and temperatures, results in two main regions which overlap in the Chiloé region (Guiler *in* STEPHENSON & STEPHENSON, 1972). Consequently, the subspecies of *Chiton magnificus* occur in geographically separated portions of the Chilean coast which are characterized by distinct environmental parameters, and the zone of intergradation of the subspecies occurs at the boundary between the two zoogeographic subprovinces.

As the synonymy indicates, several names have been applied to this species. BARNES (1824) first named it *Chiton striatus*, but this name is preoccupied by *C. striatus* Fisher von Waldheim, 1807. The next available name appears to be *Chiton latus* Sowerby, 1825, although LOWE (1825) in the same year used the name for a different species. DALL (1909) stated that Sowerby's name appeared in January, and that Lowe's name was introduced in April. BOONE (1933) utilized Sowerby's name, not for the Chilean species, but for *Chiton stokesii* Broderip, which he misidentified. SMITH & FERREIRA (1977) noted Boone's misidentification and used the name *C. latus* Sowerby for the Galápagos species. KAAS & VAN BELLE (1980) employed the name *C. striatus* Barnes, 1824, but they did not recognize that this name is preoccupied. Actually, the South American species in question is best known by the name *C. magnificus* Deshayes, the name used by PILSBRY (1893), who believed that Sowerby's name was preoccupied, and for this reason it is used herein; a petition to conserve the well-known name "*magnificus* Deshayes" will be submitted to the International Commission on Zoological Nomenclature (Bullock, in preparation).

OTAÍZA & SANTELICES (1985) observed that along the central Chilean coast *Chiton magnificus* [as *C. latus* Sowerby] is greatest in abundance in pools and boulder fields with a large amount of water exchange. They reported that the largest individuals occur in the more exposed habitats while smaller examples are found in more sheltered areas.

Distribution: *Chiton magnificus magnificus* ranges from Peru south to Bahía Tictoc, Chiloé Province, Chile (Figure 76).

Locality records: PERU: (ANSP, RNHL, ZMHU); Isla San Lorenzo (ZMK). CHILE: Arica (ZMA); Mejillones (MCZ); Coquimbo (ANSP, USNM); Coquimbo Bay (BMNH); Valparaiso (numerous records); Talcahuano (RNHL); Calbuco (RNHL); Isla de Chiloé (NMB, RNHL, ZMHU, ZMK); Archipiélago de los Chonos (ZMHU); Bahía Tictoc, Chiloé Prov., in rock pools (USNM).

Chiton (*Amaurochiton*) *magnificus bowenii* King, 1832

(Figures 55, 56, 71, 76)

Chiton bowenii KING, 1832:5:338 (ad oras insulae Tierra del Fuego et in freto Magellanico; syntypes BMNH); REEVE, 1847:pl 2, sp. 9; PILSBRY, 1893:164, pl. 38, fig. 23.
Chiton (*Lophyrus*) *bowenii* King. CLESSIN, 1903:3, pl. 4, fig. 2.
Chiton latus Sowerby. LELOUP, 1956 [in part]:50.
Chiton bowenii King. KAAS & VAN BELLE, 1980:18.

Description: Animal elongate, reaching 86 mm in length and 40 mm in width. Valves carinate, angle about 100°. Anterior valve and post-mucronal slope of posterior valve straight. Mucro rather pointed, anteriorly acentric on posterior valve. Jugal and central regions smooth. Lateral triangle smooth, with occasional specimens showing evidence of obsolete, radiating ribs. Terminal areas smooth or with obsolete radiating ribs. Shell color black, brown or reddish brown with occasional lighter streaks. Girdle black. Interior of valves white.

Tegmentum: Dorsal layer of suprategmentum thick; ventral layer with numerous small, horizontal canals. Subtegmentum with medium-sized, close-packed canals with occasional smaller canals above, reduced at jugum.

Figure 77

Distribution of *Chiton* (*Amaurochiton*) *cumingsii* Frembly.

Esthete pores: Similar to *Chiton m. magnificus.*

Articulamentum: Similar to *Chiton m. magnificus.* Slit formula 14/1/16–17.

Girdle scales: Relatively small considering the large adult size of the animal, rounded, glossy; ventro-lateral sculpture of thin ribs restricted to areas hidden by overlapping scales. Dorso-lateral areas smooth (Figure 71).

Radula: [not observed].

Remarks: Typical *Chiton m. bowenii* can easily be distinguished from the northern *C. m. magnificus* by its more elongate form, highly arched valves, and small girdle scales (see remarks under *C. magnificus magnificus*). *Chiton m. bowenii* may be reddish, black, or a combination of both colors.

Distribution: Most specimens of *Chiton m. bowenii* in museum collections lack precise locality data and little can be said concerning its range in relation to *C. m. magnificus.* On the basis of well-documented material, *Chiton magnificus bowenii* extends from Castro Inlet, Isla de Chiloé, Chile, south to the Strait of Magellan (Figure 76).

Locality records: CHILE: Castro, Isla de Chiloé (USNM); Port San Pedro, Isla de Chiloé (ZMA, RNHL); Port Otway (USNM); Strait of Magellan (ANSP, NMB, IRSN, MCZ, ZMNH); Terra del Fuego (BMNH).

Chiton (*Amaurochiton*) *cumingsii* Frembly

(Figures 59–63, 69, 74, 77)

Chiton cumingsii FREMBLY, 1827:198, suppl. pl. 16, fig. 3 (Valparaiso; location of type unknown); PLATE, 1899: 46, 57, pl. 3, figs. 179–184, pl. 4, figs. 185–189; DALL, 1909:247; MARINCOVICH, 1973:43, fig. 97.

Chiton cummingii [*sic*] Frembly. GRAY, 1828:6.

Chiton cumingii [*sic*] Frembly. SOWERBY, 1840a:3, figs. 32, 51; REEVE, 1847:pl. 1, sp. 2b [not 2a which is *C. viridis* Spengler]; DALL, 1879:79, 126, pl. 3, fig. 25 [radula].

Amaurochiton cumingi [*sic*] (Frembly). THIELE, 1893:363, pl. 30, fig. 5 [radula].

Chiton cumingi [*sic*] Frembly. PILSBRY, 1893:164, pl. 30, figs. 29–31.

Chiton (*Lophyrus*) *cumingii* [*sic*] Frembly. CLESSIN, 1903:6, pl. 5, fig. 2.

Chiton cumingsi [*sic*] Frembly. BERGENHAYN, 1930:29, pl. 7, fig. 65; LELOUP, 1956:47; KAAS & VAN BELLE, 1980: 35; OTAÍZA & SANTELICES, 1985:229–240 [vertical distribution].

Description: Animal reaching 45 mm in length and 30 mm in width. Angle of valves 100–120°. Anterior valve straight; post-mucronal slope of posterior valve slightly concave. Mucro blunt, anteriorly acentric on posterior valve. Jugal and central areas with a number of low ribs, more prominent on jugum. Lateral triangle slightly raised, with five to seven low, nodular, radiating ribs which occasionally bifurcate. Shell color yellowish white with concentric brown bands crossing lateral triangle longitudinally, then proceeding antero-medially over ribs of central area. Irregular, thin brown concentric bands on terminal valves. Occasional dark brown streaks on jugum. Girdle light olive green. Interior of shell white with some dull green in posterior depression.

Tegmentum: Suprategmentum thick; subtegmentum having numerous somewhat close-packed canals of moderate size, with occasional smaller canals above, and greatly reduced at jugum (Figure 63).

Esthete pores: Megalopores large, round to ovate, with slightly beveled edges, about 1.5 times as large as the irregularly ovate micropores (Figure 62).

Articulamentum: Central depression of intermediate valves with scattered slits within jugal tract. Primary slit-ray well developed with slits on callus and small holes, occasionally two per longitudinal row, in posterior depression. Secondary slit-ray present. Insertion teeth deeply pectinate. Slit formula 14/1/16.

Girdle scales: Roundly triangular, at times slightly pointed. Ventro-lateral areas with fine, well-spaced longitudinal ribs. Dorso-lateral areas smooth (Figure 69).

Radula: Central tooth moderately narrow, deeply cup-shaped, rounded distally, and tapering basally. Pad of centro-lateral large. Wing of major lateral rectangular, distal end thickened. Denticle cap rectangular, only slightly pointed distally; black tab moderately extended, narrowing distally. Magnetite touches tab only distally; much of rest of tab surrounded by tan substance (Figure 74).

Remarks: The distinctive coloration differentiates this species from all other eastern Pacific *Chiton* (see also remarks under *C.* (*A.*) *magnificus*). A few specimens in the collection of the Museum of Comparative Zoology approach *C. magnificus* in form and, in one case, a specimen from Caldera, only the color pattern distinguishes it. While some specimens of *C. cumingsii* are ovate and lowly arched, others are elongate and quite carinate. Occasional specimens are nearly black. When adequate samples of this species are available, it will be interesting to compare the intraspecific variation of *C. cumingsii* with that of the sympatric *C. magnificus*.

Considering the great conchological contributions made by Mr. Hugh Cuming (DANCE, 1966), including the collection of chiton species new to science and large, valuable collections from the west coast of South America, it is very appropriate that a prominent polyplacophoran was named in his honor. Unfortunately, the species was named "after my friend Mr. Cumings [*sic*]" and this misspelling must be maintained as the correct original spelling (see remarks under *C. stokesii*).

According to OTAÍZA & SANTELICES (1985), in central Chile *Chiton cumingsii* is found in pools and boulder fields where the amount of water exchange is not great. They observed that *C. cumingsii* coexists with *Ischnochiton pusio* (Sowerby, 1832) and *Tonicia elegans*, form *lineolata* (Frembly, 1827) [=*Tonicia chilensis glabra* (Clessin, 1903), *fide* KAAS & VAN BELLE (1908)]. MARINCOVITCH (1973) reported that at Iquique, Chile, *C. cumingsii* is found in the lower intertidal zone on the undersides of rocks.

Distribution: *Chiton cumingsii* occurs from Peru south to Calbuco, Chiloé Prov., Chile (Figure 77).

Locality records: PERU: (BMNH, MCZ, MNHNP); Tumbes (MCZ, ZMHU); Paita (MCZ, RNHL); Salaverry (USNM); Callao (MCZ, USNM, ZMHU); La Punta, Callao (USNM); Isla San Lorenzo (MCZ, NRS, USNM); Pucusana (USNM); Island near Pucusana (MCZ); Bahía de la Independencia (ANSP); Matarini (ZMK); Islay (BMNH). CHILE: Arica (ANSP, USNM); Iquique (ANSP, MCZ, USNM, ZMA, ZMHU); off military base, Iquique (USNM); Punta Cobija (MNHNP); Antofagasta (RNHL, USNM, ZMK); near Universidad del Norte, Antofagasta (MCZ); rock pools, Antofagasta (ZMK); Caldera (MCZ); Coquimbo (ANSP, MNHNP, USNM); near Montemar Marine Laboratory, Viña del Mar (MCZ); Valparaiso (numerous records); Talcahuano (MCZ); Calbuco (RNHL).

Chiton (*Amaurochiton*) *glaucus* Gray, 1828

(Figures 66, 67, 70, 75, 78–83)

Chiton glaucus GRAY, 1828:5 (locality unknown; holotype in BMNH); HUTTON, 1880:112; HUTTON, 1882:129, pl. 16, fig. f [radula]; FISCHER, 1978:44; KAAS & VAN BELLE, 1980:54.

Chiton viridis QUOY & GAIMARD, 1835:383, pl. 74, figs. 23–28 (New Zealand; syntypes MNHNP). *Non* Spengler, 1797; *non* Monterosato, 1875; *non* (Chemnitz) Clessin, 1904.

Chiton quoyi DESHAYES, 1836:509 (new name for *C. viridis* Quoy and Gaimard, 1835, *non* Spengler, 1797); REEVE, 1847:pl. 13, sp. 68; PILSBRY, 1893:172, pl. 37, figs. 6–8; SUTER, 1897:194; SUTER, 1899:62, 63; NIERSTRASZ, 1905b:150.

Chiton tenuistriatus SOWERBY, 1840a:fig. 135 (no locality given [Wellington, New Zealand, herein selected as type locality]; location of type unknown); SOWERBY, 1840b: 290; PILSBRY, 1893:188, pl. 38, figs. 27, 28. *Non Amaurochiton tenuistriatus* "Sowerby" Thiele, 1893 [=*C. magnificus magnificus* Deshayes]; *non Chiton* (*Clathropleura*) *tenuistriatus* "Sowerby" Thiele, 1910 [=*Rhyssoplax salihafui* (Bullock)].

Chiton aquatilis REEVE, 1847:pl. 13, sp. 73 (locality unknown [Wellington, New Zealand, herein selected as type locality]; type in BMNH); PILSBRY, 1893:169, pl. 38, figs. 33, 34; KAAS & VAN BELLE, 1980:9 [stated to be from Tsu-Sima, Japan].

Lophyrus glaucus (Gray). ANGAS, 1867:222.

Poeciloplax glauca (Gray). THIELE, 1893:365, pl. 30, fig. 11 [radula].

Chiton aereus "Reeve" SUTER, 1897:195 [misidentification, *fide* IREDALE & HULL (1932)].

Chiton (*Lophyrus*) *viridis* Quoy & Gaimard. CLESSIN, 1903: 4, pl. 4, fig. 4.

Chiton (*Lophyrus*) *aquatilis* Reeve. CLESSIN, 1903:45, pl. 16, fig. 7.

Chiton (*Lophyrus*) *quoyi* Deshayes. CLESSIN, 1904:115, pl. 40, fig. 4.

Chiton quoyi, var. *limosa* (Suter) NIERSTRASZ, 1905b:151 (Neu-Seeland [type locality herein restricted to Manukau Harbour]; location of type unknown).

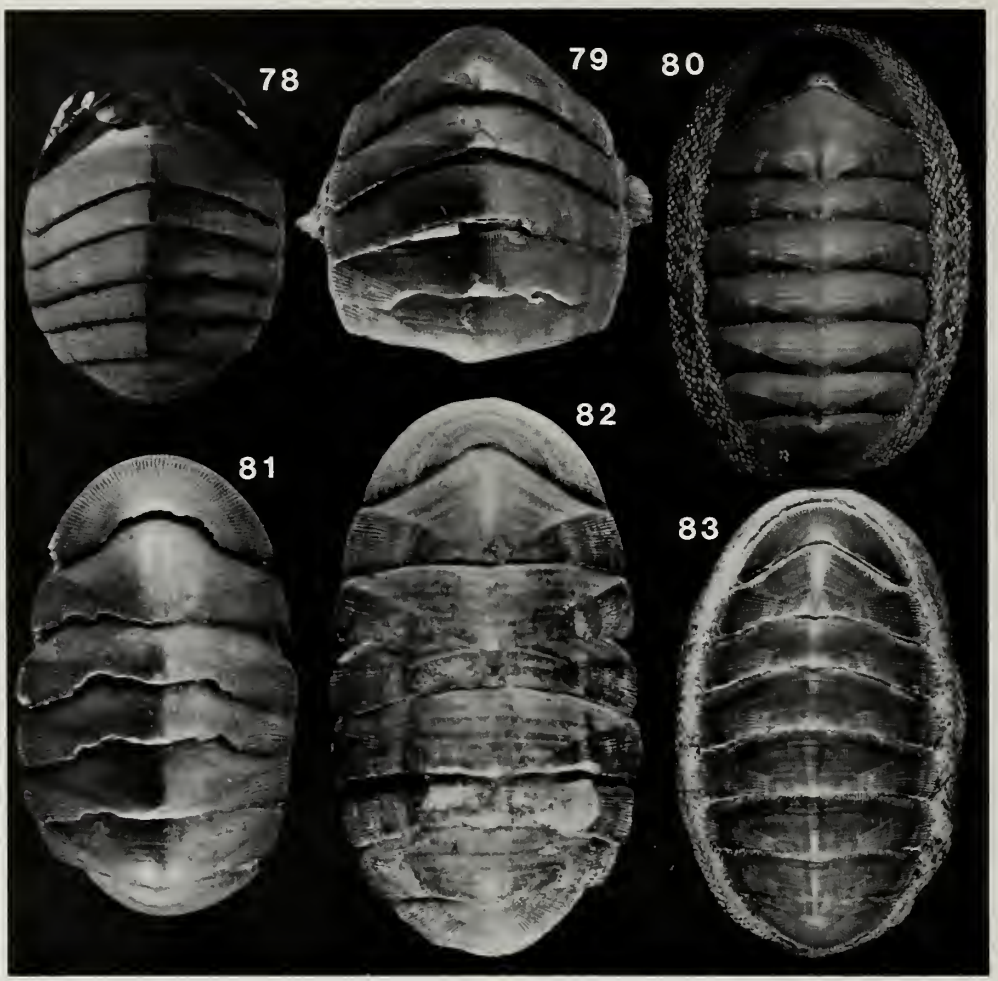
Chiton quoyi limosus SUTER, 1905:69 (Manukau Harbour, N.Z.; lectotype, selected by BOREHAM [1959], N.Z. Geol. Survey TM 1242 [not seen]).

Chiton (*Poeciloplax*) *quoyi* Deshayes. THIELE, 1909:2; THIELE, 1929:20.

Amaurochiton glaucus (Gray). IREDALE, 1914:38; IREDALE, 1915:422, 426; MAY, 1921:34; May, 1923:37; IREDALE & HULL, 1926:256, pl. 37, figs. 1, 22; IREDALE & HULL, 1927:119, pl. 15, figs. 1, 22; IREDALE & HULL, 1932: 150, pl. 9, figs. 1–7, pl. 10, fig. 10 [extensive synonymy]; ALLAN, 1959:228.

Rhyssoplax aquatilis (Reeve). IS. TAKI, 1962:45; IW. TAKI, 1964:412.

Description: Animal reaching 45 mm in length and 30 mm in width. Angle of valves about 100°. Anterior valve and post-mucronal slope of posterior valve straight to slightly convex. Mucro blunt, anteriorly acentric on posterior valve. Jugal and central regions with numerous fine longitudinal ribs. Lateral triangle barely raised, with 12–18 fine radiating ribs which at times bifurcate. Terminal areas with similar fine radial sculpture. Shell color variable, from all white to various shades of brown and green. Girdle variegated, appearing light olive green; scales aquamarine or light blue, some bordered with light reddish brown. Interior of valves bluish white; apophyses white; jugal tract light reddish brown; posterior slope of callus reddish brown.



Explanation of Figures 78 to 83

Shells of *Chiton* (*Amaurochiton*) *glaucus* Gray.

Figure 78. **Holotype** of *Chiton glaucus* Gray, locality unknown (BMNH).

Figures 79 and 81. **Syntypes** of *Chiton viridis* Quoy & Gaimard, New Zealand (MNHNP) (Figure 79, 17 mm length; Figure 81, 30 mm length).

Figure 80. Little Manly, Auckland, New Zealand (USNM 681351) (22.5 mm).

Figure 82. **Syntype** of *Chiton aquatilis* Reeve, locality unknown (BMNH).

Figure 83. Army Bay, Wrangaparoa, New Zealand (RCB) (34 mm).

Tegmentum: Suprategmentum thick, ventral layer dark brown with a brown extension proceeding dorsally to each longitudinal rib. Subtegmentum moderately developed with one ventral layer of medium-sized canals with a layer of small canals above (Figure 67).

Esthete pores: Megalopores large, round, with beveled edges, about three to four times as large as ovate micropores (Figure 66).

Articulamentum: Central depression of intermediate valves with scattered transverse slits in jugal tract. Primary slit-ray with elongate slits, occasionally two per longitudinal row. Insertion teeth well grooved, not deeply pectinate. Slit formula 13/1/15.

Girdle scales: Roundly triangular. Ventro-lateral reticulate sculpture proceeds apically near margins; slight apical shelf present. Dorso-lateral area devoid of sculpture, except near apex, where some broad, rather inconspicuous nodules are seen on some scales (Figure 70).

Radula: Central tooth rather broad, cup-shaped distally, tapering somewhat basally. Pad of centro-lateral tooth oblong, smooth in appearance, constricted near base. Wing of major lateral tooth roughly triangular, pointed distally. Denticle cap quite elongate; tab long and fairly thin, conspicuously visible against surrounding amber material (Figure 75).

Remarks: *Chiton glaucus* is characterized by having fine, smooth radial ribs on the lateral triangle and terminal areas. This New Zealand species, which also occurs in southeastern Australia, is easily distinguished from the

South American *C.* (*A.*) *magnificus* by its fine sculpture and smaller size. Radular and girdle scale characteristics of *C. glaucus* lead one to the conclusion that this species does not fit as well into the subgenus *Amaurochiton* as the easily visible shell morphology would indicate. The reticular ventro-lateral sculpture of the scales (Figure 70) is not seen in other *Amaurochiton*. The radular denticle cap (Figure 75) also differs from that of other *Amaurochiton* by its more elongate form.

Though usually dark green or greenish brown, *Chiton glaucus* may exhibit an array of colors, including bright green, white, yellow, brownish orange, or reddish brown and, occasionally, variegated individuals occur.

It is surprising that this rather distinctive, commonly collected chiton was not better known to conchologists of the nineteenth century. The small type specimen of *Chiton glaucus* Gray is white (Figure 78), and it may not have appeared to be conspecific with the larger, more colorful forms. The identity of *C. tenuistriatus* Sowerby was not recognized until Bullock (1972b) noted that the brief description (Sowerby, 1840b) and the figure in the *Conchological Illustrations* (Sowerby, 1840a) refer to *C. glaucus* Gray. Thiele (1910a) used Sowerby's name "*tenuistriatus,*" but in fact he had before him an undescribed species later introduced as *Chiton salihafui* Bullock, 1972. Although it is not mentioned under *Chiton quoyi* [=*C. glaucus*], Pilsbry (1893:188) reported that *C. tenuistriatus* was the same as *C. quoyi* or *C. nigrovirens* [*sic*]; the latter species is properly assigned to the genus *Radsia* (Bullock, 1988). The two syntypes of *Chiton aquatilis* Reeve, which closely match the figure in the *Conchologia Iconica,* are also conspecific with *C. glaucus* (see Figure 82). The label on the back of the British Museum (Natural History) tablet of *C. aquatilis* states the locality, with a query, as Japan, perhaps because the Damon specimen of "*aquatilis*" offered for sale was supposedly from Tsu-Sima, Japan. This comment may explain why Kaas & Van Belle (1980) gave Tsu-Sima as the type locality. According to Carpenter (*in* Pilsbry 1893:169), *C. aquatilis* "may equal my *C. densiliratus* in poor condition," but the latter name, validated by Pilsbry, is now used for an Indonesian-Philippine species which does not belong in *Amaurochiton,* but in *Rhyssoplax*.

Distribution: *Chiton glaucus* is found in New Zealand and southern Tasmania (Figure 84). May (1923) noted that it is abundant in the Derwent Estuary, Tasmania, and that it was "probably introduced on New Zealand oysters." Iredale & Hull (1926, 1927) also thought it was introduced to Tasmania. Allan (1959:228) stated: "the New Zealand conchologist, Mr. A. W. B. Powell, considers this [introduction] may have been brought about by means of shipping as in New Zealand the species is known to cling to hulls of boats."

Locality records: Australia: *Tasmania*: (ZMK); Hobart (IRSN, MCZ, WAM, ZMHU); Derwent (WAM); Derwent Estuary (ANSP, MCZ); Brown's River, mouth of Derwent River (ANSP, USNM). New Zealand: *North Id.*: North Cape (ZMK); Waipu (MCZ); Takapuna (BMNH); Auckland (ANSP, NMB, IRSN, MCZ, USNM, USNM, ZMA); Hobson Bay, Parnell side, Auckland (MCZ); Ponui Id., E of Auckland; Slipper Id. (both ZMK); Tauranga (ZMHU); Pilot Bay, Tauranga (DMNH); Mt. Maunganui (ANSP); Mahia Peninsula (NRS, ZMK); Wellington (MCZ, RNHL, USNM); reef islet, Wellington (MCZ); New Plymouth; Kawhia Harbour (both IRSN); Manukau Harbour (ANSP, IRSN, RNHL, ZMHU); *South Id.*: Lyttelton (IRSN); Akaroa (IRSN, ZMK); Otago Harbour (NRS); near marine laboratory, Portobello, Otago Harbour (MCZ); Paterson Inlet, Stewart Id. (ZMK, NRS); Sumner (RNHL, ZMA).

Figure 84

Distribution of *Chiton* (*Amaurochiton*) *glaucus* Gray.

Subgenus *Diochiton* Thiele, 1893

Scutigeruli Meuschen, 1787:240 [invalid introduction (see under Remarks)].

Scutigeratus "Meuschen" Paetel, 1875:187 [error for *Scutigerulus*].

Diochiton Thiele, 1893:364. Type species by monotypy, *Diochiton albilineatus* [*sic*] (Sowerby) [*sic*] [=*Chiton albolineatus* Broderip & Sowerby].

Scuterigulus [*sic*] Meuschen. A. G. Smith, 1960:165 [misspelling; as a synonym of *Chiton*]. Type species designated to be *Chiton squamosus* Linnaeus, 1758 [*sic*] [invalid introduction and type designation].

Scutigerulus Meuschen. Van Belle, 1978:20; Van Belle, 1983:122 [both in synonymy with *Chiton*].

Description: Adults attaining 123 mm in length. Valves rounded. Jugum smooth; central areas smooth or with narrow longitudinal ribs which may be more prominent near the diagonal line. Lateral triangle elevated, rarely depressed; smooth or with radiating rows of nodules which may be arranged in a checkered pattern, or form radial ribs. Girdle scales variable in size; dorso-lateral areas smooth or with pustules of various sizes.

Remarks: Thiele (1893) proposed *Diochiton* on the basis of differences noted in radular morphology, as well as

factors pertaining to the distribution and ecological niche of *Chiton albolineatus*. Although these differences alone do not justify the use of *Diochiton*, the name is used for a group of *Chiton* species characterized by their medium to large size, highly pectinate insertion teeth, and, particularly, their smooth jugal and usually smooth central regions. THIELE (1909) synonymized his name *Diochiton* with *Chiton*. The present subgeneric usage differs from that of THIELE (1929), who utilized *Diochiton* as a section of *Chiton s.s.*, and SMITH (1960) and VAN BELLE (1978, 1983) who considered *Diochiton* to be a synonym of *Chiton*. The seven species included in the subgenus are: (1) the Panamic *C. albolineatus* Broderip & Sowerby, the type species of *Diochiton*; (2) the *C. squamosus* species group, with *C. goodallii* Broderip from the Galápagos Islands, *C. marquesanus* Pilsbry from the Marquesas Islands, and the West Indian species, *C. squamosus* Linnaeus; (3) *C. viridis* Spengler from the Caribbean; and (4) the *C. marmoratus* species group, which includes the Panamic *C. articulatus* Sowerby and the West Indian *C. marmoratus* Gmelin.

In an historical sense, the name *Scutigerulus* belongs in the synonymy of *Diochiton*, although it appears that the name has never been properly introduced. The introduction of "*Scutigeruli*" by MEUSCHEN (1787) is invalid according to ICZN Art. 11g because the name is not in the nominative singular or treated as such. The name first appeared in its correct form in the supplement of HERRMANNSEN's (1852) *Indicis generum malacozoorum*, and NEAVE (1940) recorded the date and authorship of *Scutigerulus* to be HERRMANNSEN (1852); however, the usage of this name, although in the nominative singular, does not constitute a valid introduction because Herrmannsen used the name only as a synonym of *Chiton* and *Scutigerulus* has never been "adopted as the name of a taxon or treated as a senior homonym" (ICZN Art. 11e). When Meuschen introduced "*Scutigeruli*," he included three Linnaean species (*C. fascicularis, C. squamosus,* and *C. punctatus*) and one new species (*S. angulatus*); SMITH (1960) erroneously accepted Meuschen's name and selected *C. squamosus* Linnaeus as the type species, but this still does not constitute a valid introduction because the name is listed in synonymy with *Chiton*. KAAS & VAN BELLE (1980) synonymized *Scutigerulus* [*sic*] *angulatus* Meuschen, 1797, with *C. squamosus* Linnaeus, 1764. VAN BELLE (1983:122) recorded *C. squamosus* as the type species of *Scutigerulus* because it was the "only species attributable to genus *Chiton*."

KEY TO THE SPECIES OF THE SUBGENUS *Diochiton*

1. Lateral triangle smooth or with faint radiating ribs 2
   Lateral triangle with well-developed radiating ribs or rows of nodules 4
2. Girdle uniformly colored, scales brown or dark yellowish brown; valves dark brown .. *C.* (*D.*) *goodallii*
   Girdle alternately banded dark and light green; valves usually with longitudinal dark streaks on central area and jugum 3
3. Muscle scars posterior to apophyses lacking dark blue-green coloration; valves usually roundly convex; jugal sinus relatively wide; longitudinal brown markings of central area usually quite numerous *C.* (*D.*) *marmoratus*
   Muscle scars posterior to apophyses with dark blue-green coloration; valves flattened; jugal sinus moderately narrow; longitudinal dark brown markings of central area usually present as a few broad bands near jugum ..... *C.* (*D.*) *articulatus*
4. Lateral triangle sharply elevated; central area with numerous fine ribs which do not extend to anterior margin ..... *C.* (*D.*) *viridis*
   Lateral triangle flattened or not sharply elevated; central area quite smooth 5
5. Lateral triangle and terminal areas with white radiating ribs ..... *C.* (*D.*) *albolineatus*
   Lateral triangle and terminal areas with radiating rows of small nodules the same color as background 6
6. Valves uniformly dark green; girdle with dark and light green scales, not banded .. *C.* (*D.*) *marquesanus*
   Valves cream to buff; central areas with dark greenish brown longitudinal streaks; girdle alternately banded light green and cream white .... *C.* (*D.*) *squamosus*

Chiton (*Diochiton*) *albolineatus* Broderip & Sowerby, 1829

(Figures 85–87, 90, 91, 99, 104, 109)

Chiton albolineatus BRODERIP & SOWERBY, 1829:368 (Mazatlán; type in BMNH? [not found]); PILSBRY, 1893: 160, pl. 32, fig. 57; KEEN, 1958:517, fig. 1; Thorpe [*in* KEEN], 1971:864, fig. 2; ABBOTT, 1974:405; HAAS & KRIESTEN, 1978:257 [esthetes]; KAAS & VAN BELLE, 1980:5.

Chiton albilineatus [*sic*] Sowerby [*sic*]. REEVE, 1847:pl. 2, sp. 11.

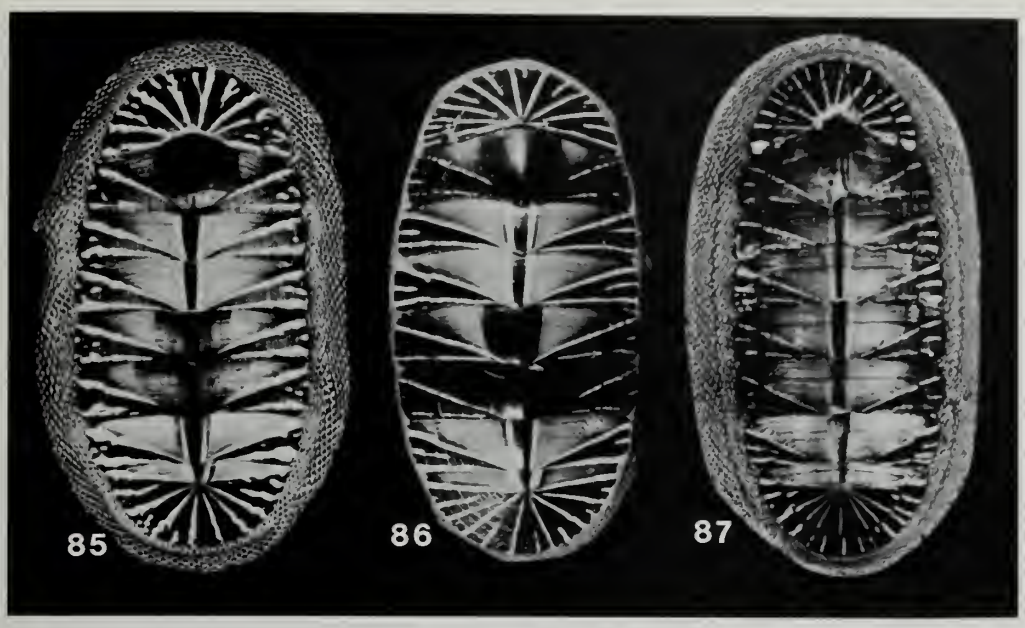
Lophyrus albolineatus (Broderip & Sowerby). CARPENTER, 1857a:317.

Diochiton albilineatus [*sic*] Sowerby [*sic*]. THIELE, 1893:365, pl. 30, fig. 10 [radula].

Chiton (*Lophyrus*) *albilineatus* [*sic*] Sowerby [*sic*]. CLESSIN, 1903:4, pl. 4, fig. 3.

Chiton albolineatus Sowerby [*sic*]. PILSBRY & LOWE, 1932: 130; ABBOTT, 1954:325.

Description: Animal reaching 36 mm in length, 19 mm in width, somewhat flattened, angle of valves about 110°. Anterior valve slightly convex; post-mucronal slope of posterior valve straight. Mucro blunt, anteriorly acentric on posterior valve. Jugal and central regions smooth. Lateral triangle barely raised, with two irregular ribs which produce nodular branches. End valves with nine to 11 irregular, low, radiating ribs which irregularly bifurcate or



Explanation of Figures 85 to 87

Shells of *Chiton* (*Diochiton*) *albolineatus* Broderip & Sowerby.

Figure 85. Acapulco, Mexico (MCZ 204335) (27 mm).

Figure 86. Acapulco, Mexico (MCZ 277763) (26 mm, slightly curled).

Figure 87. Punta Camaron, Mazatlán, Sinaloa, Mexico (SDSC) (30.5 mm).

begin anew between established ribs. Central areas olive green, jugal region lighter, with numerous transverse zigzag lines, and, occasionally with large black splotch or black band on white at jugum. Lateral triangles and terminal areas black with white radiating ribs. Girdle gray; each scale bluish gray with very light reddish brown border. Interior of valves white.

Tegmentum: Subtegmentum with moderately close-packed, medium-sized canals which enter anterior edge of intermediate valve diagonally toward mucro. Several large esthete canals among jugal teeth (Figure 90).

Esthete pores: Megalopores large, round, about two to four times as wide as the ovate micropores (Figure 91).

Articulamentum: Central depression of intermediate valve with a number of slits which extend over callus to mucral callus. Primary slit-ray well developed; slits single, oval or elongate. Secondary slit-ray present laterally. Insertion teeth deeply pectinate. Slit formula 15/1/12.

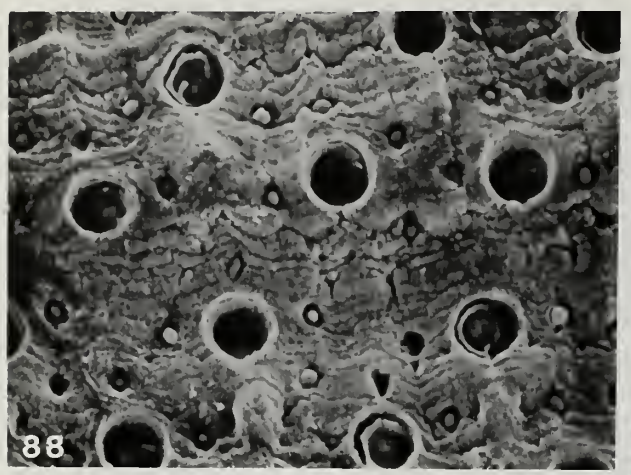
Girdle scales: Roundly triangular, relatively small. Ventro-lateral sculpture of moderately fine, occasionally anastomosing longitudinal ribs. Apical and dorso-lateral areas smooth, except for some scattered low nodules (Figure 99).

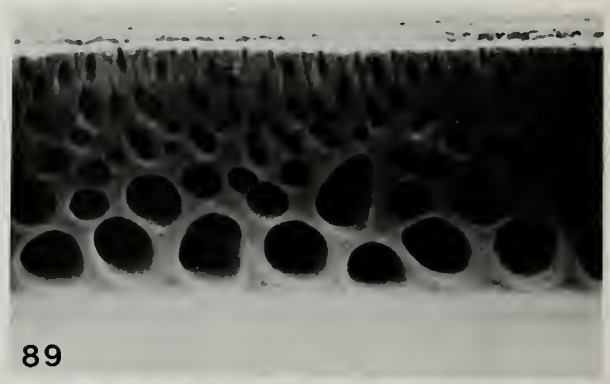
Radula: Central tooth moderately narrow, rounded distally, tapering basally. Wing of major lateral tooth paddle-like, rounded distally. Denticle cap of major lateral tooth somewhat pointed, tab elongate (Figure 104).

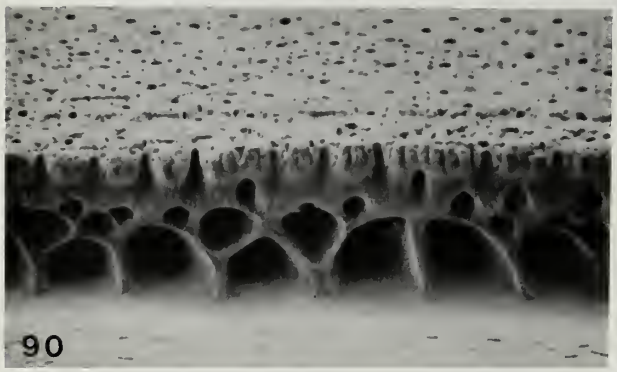
Remarks: The distinctive coloration of *Chiton albolineatus* allows immediate recognition. This Panamic-Mexican species differs from *C.* (*D.*) *articulatus* Sowerby, the only other *Diochiton* occurring along the western Central American coast, by its more highly arched valves, and by the radial ribs and nodes of the lateral triangle. In this respect, *C. albolineatus* appears to be more closely related to the *C. goodallii* species group than the *C. marmoratus* group. *Chiton albolineatus* differs from *C. goodallii* and *C. marquesanus* by its smaller size, more convex valves, and proportionately smaller girdle scales. *Chiton goodallii* has a rather smooth lateral triangle and a multiply slit insertion plate; *C. marquesanus* has more nodes on the lateral triangle and lacks any evidence of radial ribs.

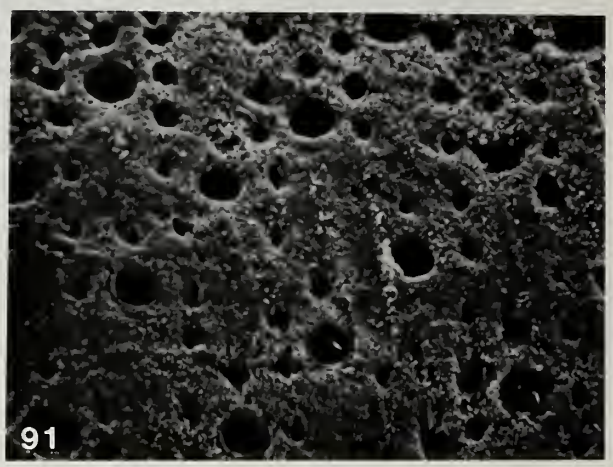
Distribution: *Chiton albolineatus* occurs from Mazatlán, near the entrance of the Gulf of California, south to southern Mexico (Figure 109). The Guatemala record listed below has not been supported by recent collecting and needs confirmation; the Guaymas record is highly questionable.

Locality records: Mexico: Guaymas (BMNH); E side of Isla Venados, NW of Mazatlán (ANSP); Mazatlán (numerous records); Chivos Id., E of breakwater, Mazatlán (ANSP); under rocks, intertidal to 12 ft [3.7 m], S jetty, Mazatlán (BMNH); rocky breakwater, S Playa, Mazatlán (ANSP); on rocks at low tide mark, N of Punta Derecha, Bahía Ola Altas, Mazatlán; Islas Tres Marias (both USNM); Manzanillo (ANSP, DMNH, USNM); Bahía Santiago, Manzanillo (DMNH); Acapulco (ANSP, MCZ, RCB, USNM). Guatemala: (USNM).









Explanation of Figures 88 to 91

Esthete pores and anterior tegmental innervation of *Chiton* (*Diochiton*) *goodallii* Broderip and *C.* (*D.*) *albolineatus* Broderip & Sowerby.

Figures 88 and 89. *C. goodallii,* Post Office Bay, Isla Santa Maria, Galápagos Ids. (USNM 522769) (Figure 88, ×344; Figure 89, ×43).

Figures 90 and 91. *C. albolineatus,* Acapulco, Mexico (RCB) (Figure 90, ×86; Figure 91, ×344).

Chiton (*Diochiton*) *viridis* Spengler, 1797

(Figures 6, 95, 102, 112–115, 122–124)

Chiton squamosus denticularis CHEMNITZ, 1788:372, pl. 173, fig. 1689 [rejected work].

Chiton viridis SPENGLER, 1797:70, pl. 6, fig. 5 (Westindien [herein restricted to St. Croix, Virgin Islands]; type in ZMK); PILSBRY, 1893:156, pl. 33, figs. 64–67; THIELE, 1910b:112; ABBOTT, 1954:325; ABBOTT, 1958:108; WARMKE & ABBOTT, 1961:219; DE JONG & KRISTENSEN, 1968:29; KAAS, 1972:114, figs. 235–238, pl. 8, fig. 1; ABBOTT, 1974:405; FERREIRA, 1978:85, figs. 9, 10; KAAS & VAN BELLE, 1980:14; LYONS, 1981:38; FERREIRA, 1985:203. *Non* Quoy & Gaimard, 1835, *non* (Chemnitz) Clessin, 1904.

Chiton luteolus WOOD, 1828:1, fig. 3 (locality unknown [herein designated to be St. Croix, Virgin Islands]; location of type unknown).

Chiton excavatus (Gray MS?) SOWERBY, 1840a:fig. 131 (no locality given [herein designated as St. Croix, Virgin Islands]; location of type unknown.

Chiton foveolatus SOWERBY, 1840a:fig. 60 (locality unknown [herein designated as St. Croix, Virgin Islands]; type assumed lost); SOWERBY, 1840b:290; REEVE, 1847:pl. 6, sp. 28.

Chiton costatus C. B. ADAMS, 1845:8 (Jamaica; lectotype, selected by CLENCH & TURNER [1950], MCZ 156026); CLENCH & TURNER, 1950:268, pl. 42, fig. 8 [lectotype]. *Non* Blainville, 1825.

Chiton (*Lophurus*) *gemmulatus* SHUTTLEWORTH, 1853:199 (St. Thomas; type in NMB).

Chiton (*Lophurus*) *excavatus* Gray. SHUTTLEWORTH, 1853: 197.

Lophyrus excavatus (Chemnitz) [*sic*]. ARANGO Y MOLINA, 1880:231.

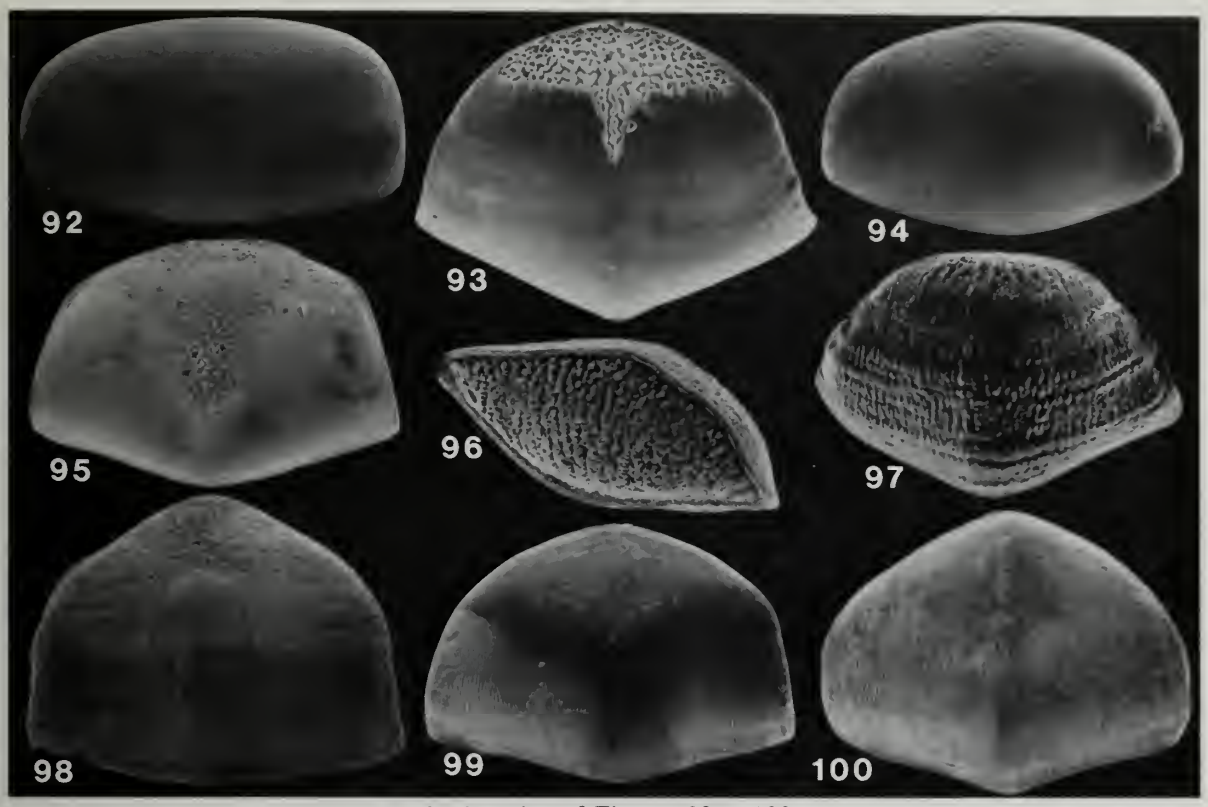
Chiton (*Lophyrus*) *foveolatus* Sowerby. CLESSIN, 1903:7, pl. 5, fig. 5.

Chiton viridis (Chemnitz). CLESSIN, 1904:108, pl. 1, figs. 4, 5 (locality unknown; location of type unknown). *Non* Spengler, 1797, *non* Quoy & Gaimard, 1835.

Chiton miltoplax REHDER, 1932:pl. 10, figs. 4, 5 [*nomen nudum*].

Chaetopleura reesi SALISBURY, 1953:41, pl. 7 (Jacksons Point, Grand Cayman; type in BMNH).

Chiton viridis, var. *rubrocarinatus* USTICKE, 1959:90 [*nomen nudum*]; USTICKE, 1969:7, fig'd. [invalid introduction *fide* ICZN Art. 16].



Explanation of Figures 92 to 100

Girdle scales of *Chiton* (*Diochiton*) and *Chiton* (*Chondroplax*).

Figure 92. *C.* (*D.*) *marmoratus* Gmelin, Pelican Cove, St. Croix, Virgin Ids. (RCB) (×44).

Figures 93. *C.* (*D.*) *articulatus* Sowerby, Acapulco, Mexico (RCB) (×55).

Figure 94. *C.* (*D.*) *squamosus* Linnaeus, Cabo Rojo Lighthouse, Puerto Rico (RCB) (×35).

Figure 95. *C.* (*D.*) *viridis* Spengler, Archers Bay, St. Lucy, Barbados (RCB) (×62).

Figures 96 and 97. *C.* (*Chondroplax*) *granosus* Frembly, locality unknown (ZMK) (Figure 96, ×50; Figure 97, ×39).

Figure 98. *C.* (*D.*) *goodallii* Broderip, Post Office Bay, Isla Santa Maria, Galápagos Ids. (USNM 522769) (×29).

Figure 99. *C.* (*D.*) *albolineatus* Broderip & Sowerby, Acapulco, Mexico (RCB) (×65).

Figure 100. *C.* (*D.*) *marquesanus* Pilsbry, Atuona Bay, Hiva-Oa, Marquesas Ids. (MCZ 83916) (×42).

Chiton rubrocarinata Usticke. USTICKE, 1971:31 [stated to be a young *C. viridis*].

Chiton tuberculatus "Linnaeus" ROMASHKO, 1984:59 [misidentification of *C. viridis* Spengler].

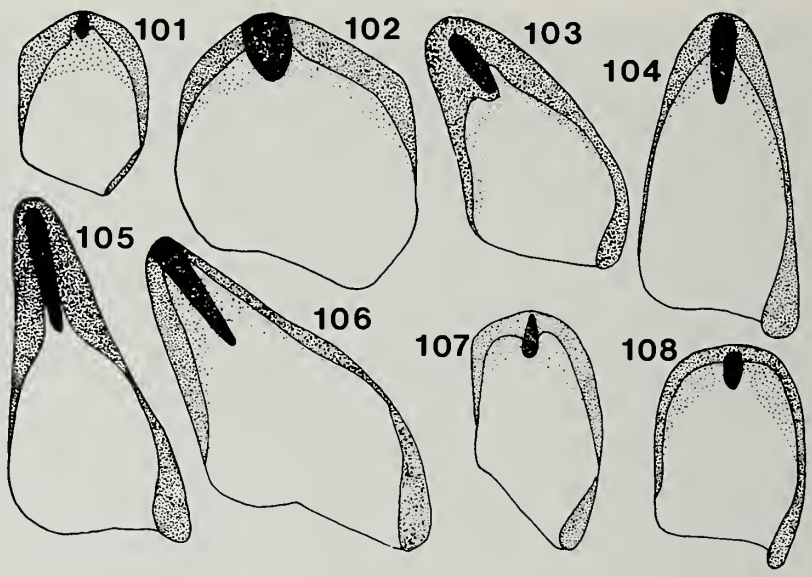
Description: Animal reaching 62 mm in length and 33 mm in width. Angle of valves about 100°. Anterior valve convex; post-mucronal slope of posterior valve slightly concave. Mucro blunt, anteriorly acentric on posterior valve. Jugal region smooth; central areas with 18 irregular, rounded ribs, well formed near lateral triangle, proceeding diagonally toward jugum, bending dorsally after reaching a secondary diagonal line. Lateral triangle with four to five nodular, radiating ribs with smooth, pitted areas between. Posterior margin of lateral triangle rake-like with sharp nodes extending posteriorly. End valves with 19–29 radiating, nodular ribs. Shell color cream white with a few longitudinal brown streaks near the jugum, a few brown splotches on central area. Lateral triangles and end valves light mauve. Girdle with alternating bands of dark and light. Interior of shell white.

Tegmentum: Upper layer of suprategmentum lighter in color; subtegmentum with large, close-packed canals with occasional smaller canals above. Subtegmentum reduced, but present at jugum (Figure 123).

Esthete pores: Megalopores large, with beveled edges, two to three times as wide as round to ovate micropores (Figure 122).

Articulamentum: Central depression of intermediate valves with numerous slits. Primary slit-ray present; slits single, large; secondary slit-ray well developed. Insertion teeth deeply pectinate. Slit formula 14/1/11.

Girdle scales: Relatively small, roundly triangular. Ventro-lateral sculpture of extremely find occasionally anastomosing, longitudinal ribs. Apical and dorso-lateral areas, the regions not covered by overlapping scales, with nu-



Explanation of Figures 101 to 108

Representative denticle caps of *Chiton* (*Diochiton*) and *Chiton* (*Chondroplax*).

Figure 101. *C.* (*D.*) *squamosus* Linnaeus, Cabo Rojo Lighthouse, Puerto Rico (RCB).

Figure 102. *C.* (*D.*) *viridis* Spengler, Arrecife Media Luna, off La Parguera, Puerto Rico (RCB).

Figure 103. *C.* (*Chondroplax*) *granosus* Frembly, near Papudo, N of Valparaiso, Chile (MCZ).

Figure 104. *C.* (*D.*) *albolineatus* Broderip & Sowerby, La Paz, Baja California (MCZ 86770).

Figure 105. *C.* (*D.*) *marquesanus* Pilsbry, Baie de Contrôleux, Nuka Hiva, Marquesas Ids. (USNM).

Figure 106. *C.* (*D.*) *goodallii* Broderip, Post Office Bay, Isla Santa Maria, Galápagos Ids. (USNM 522769).

Figure 107. *C.* (*D.*) *articulatus* Sowerby, Acapulco, Mexico (RCB).

Figure 108. *C.* (*D.*) *marmoratus* Gmelin, rocks W of Bath, Maguaripe Bay, Trinidad (MCZ).

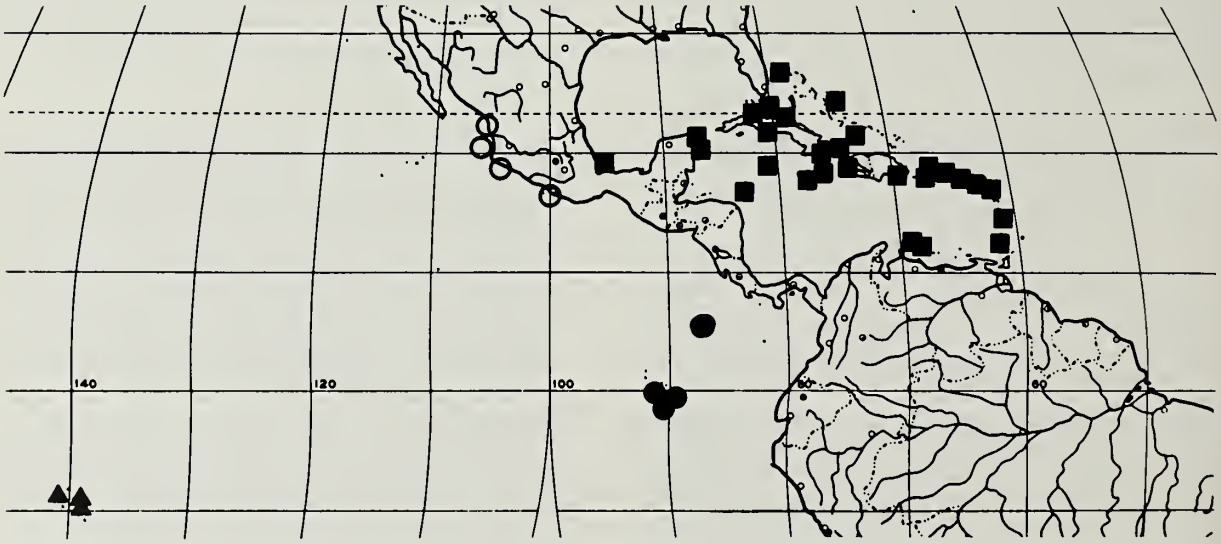
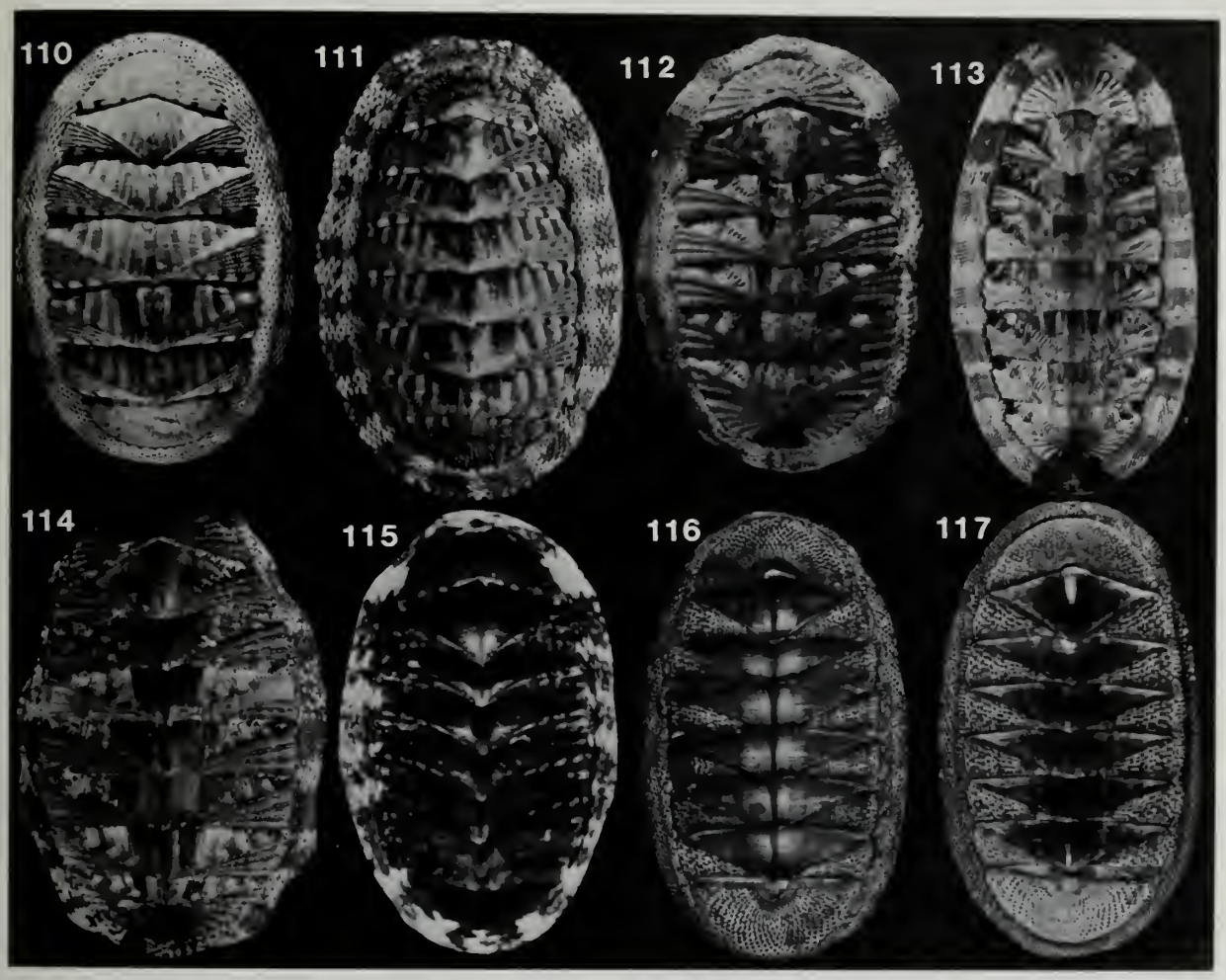


Figure 109

Distribution of *Chiton* (*Diochiton*) *albolineatus* Broderip & Sowerby (○), *C.* (*D.*) *goodallii* Broderip (●), *C.* (*D.*) *squamosus* Linnaeus (■), and *C.* (*D.*) *marquesanus* Pilsbry (▲).



Explanation of Figures 110 to 117

Shells of *Chiton* (*Diochiton*) *squamosus* Linnaeus, *C.* (*D.*) *viridis* Spengler, and *C.* (*D.*) *marquesanus* Pilsbry.

Figure 110. **Syntype** of *Chiton marmoreus* (Chemnitz) Reeve [=*C. squamosus* Linnaeus], West Indies (BMNH) (52 mm) [note: only 7 valves].

Figure 111. *C.* (*D.*) *squamosus,* Guantanamo Bay, Cuba (RCB) (44 mm).

Figure 112. *C.* (*D.*) *viridis,* E Salt Cay, near Nassau, New Providence Id., Bahama Ids. (MCZ 204310) (31 mm).

Figure 113. *C.* (*D.*) *viridis,* South Bimini, Bahama Ids. (RCB) (59.5 mm).

Figure 114. *C.* (*D.*) *viridis,* Galeta Id., Panama (RCB) (31 mm, partially curled).

Figure 115. *C.* (*D.*) *viridis,* Foster Pt., Great Swan Id. (J. Britton) (7 mm), immature specimen.

Figure 116. *C.* (*D.*) *marquesanus,* Atuona Bay, Hiva-Oa, Marquesas Ids. (MCZ 83916) (61 mm).

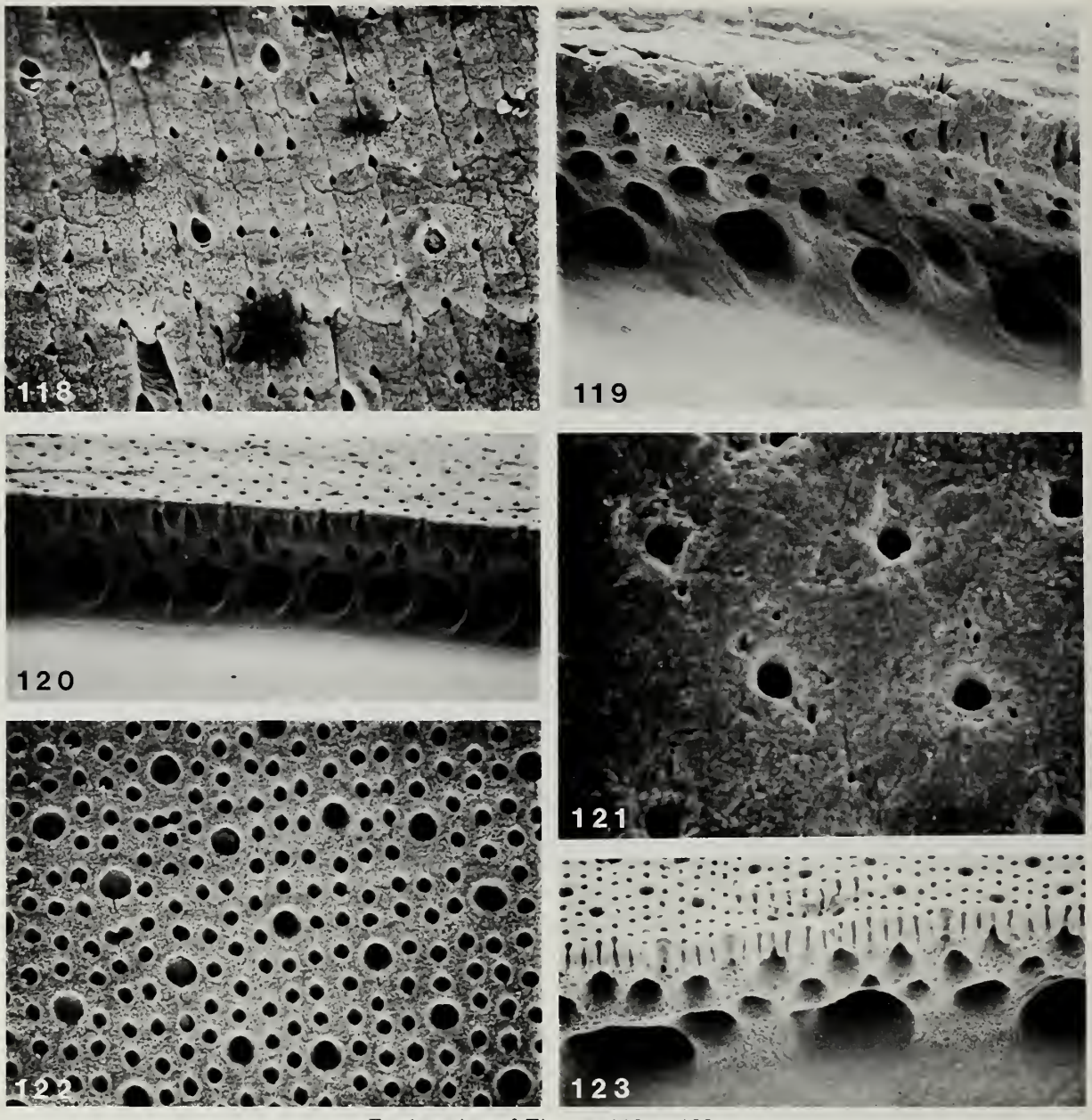
Figure 117. *C.* (*D.*) *marquesanus,* Eiao Id., Marquesas Ids. (BMNH 1952.11.10.76) (66 mm).

merous scattered pustules of rather small, but varying size. Apical shelf present, but narrow (Figure 95).

Radula: Central tooth moderately narrow, widest at middle of shaft, tapering basally; cup-shaped distally. Pad of centro-lateral oblong, conspicuous; wing of major lateral squat, rounded distally; denticle cap rather squat, cutting edge rounded; black tab nearly tear-shaped (Figure 102).

Remarks: In size and general coloration, *Chiton viridis* most closely resembles the sympatric *C. squamosus,* but differs from the latter by its relatively smaller scales and possession of irregular longitudinal sculpture on the central areas near the diagonal line. *Chiton viridis* is easily differentiated from the sympatric *C. tuberculatus* by lacking the strong longitudinal ribs on the central areas and the bold nodular ribs of the lateral triangle and terminal areas.

Chiton viridis is not commonly collected in large numbers, probably because it lives subtidally. It is not rare, however, as the numerous locality records attest. The many names applied to this species resulted from poor represen-



Explanation of Figures 118 to 123

Esthete pores and anterior tegmental innervation of *Chiton* (*Diochiton*) *squamosus* Linnaeus, *Chiton* (*Diochiton*) *marquesanus* Pilsbry, and *Chiton* (*Diochiton*) *viridis* Spengler.

Figures 118 and 119. *C.* (*D.*) *squamosus*, Guantanamo Bay, Cuba (RCB) (Figure 118, ×328; Figure 119, ×82).

Figures 120 and 121. *C.* (*D.*) *marquesanus*, Atuona Bay, Hiva-Oa, Marquesas Ids. (MCZ 83916) (Figure 120, ×41; Figure 121, ×328).

Figures 122 and 123. *C.* (*D.*) *viridis*, Archers Bay, St. Lucy, Barbados (RCB) (Figure 122, ×328; Figure 123, ×164).

tation in early collections, poor figures in the literature and, above all, because of the great difference between the young and adult specimens, a feature which baffled many conchologists. The young are brightly colored with carmine or pink and lack the characteristic adult sculpture (Figure 115). Juveniles were described as new species by C. B. Adams (1845), Shuttleworth (1853), Rehder (1932, figure only), Salisbury (1953), and Usticke (1959, 1969, 1971, all invalid introductions). Salisbury even placed his "species" in the genus *Chaetopleura* of the family Chaetopleuridae!

In Puerto Rico *Chiton viridis* lives under stones at the low water mark, along with *C. tuberculatus*, and under coral slabs in shallow water (1–2 m). In Panama *C. viridis* is always found subtidally under slabs of coral covered by fire coral or associated with sea urchin burrows, while *C.*

Figure 124

Distribution of *Chiton* (*Diochiton*) *viridis* Spengler.

tuberculatus and *C. marmoratus* are found low in the splash zone.

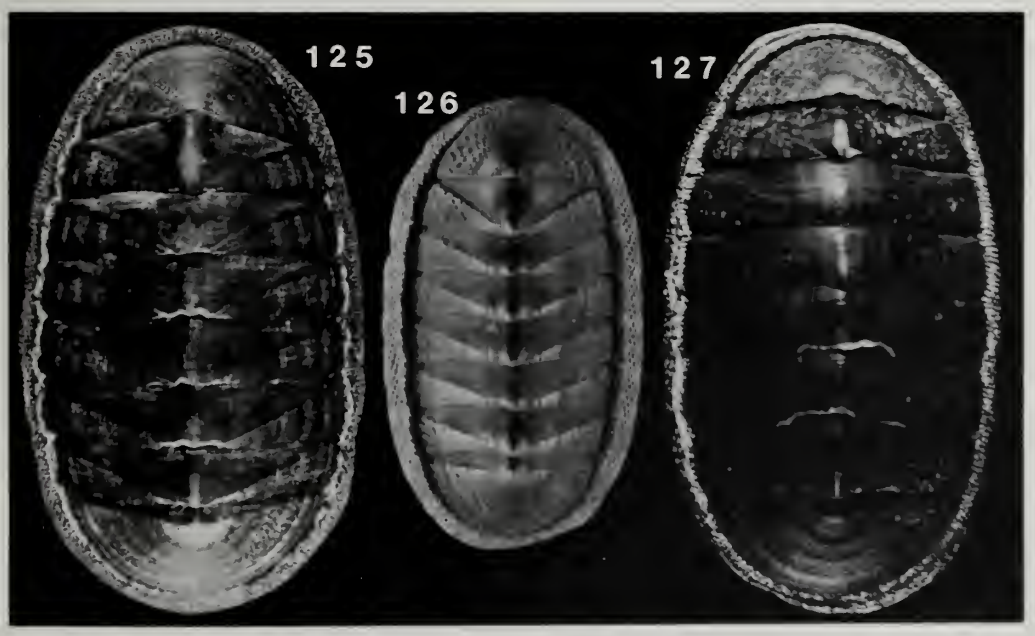
SAMPSON (1895) reported in detail on the musculature of "*Chiton viridis* Spengler," but the identification of the specimens she used cannot be verified. Her specimens were collected in Jamaica, where all species of West Indian *Chiton* occur. Her simple, unlabelled outline drawing of chiton valves could possibly represent *C. tuberculatus*.

Distribution: *Chiton viridis* is found from the Florida Keys and the Bahama Islands south to Trinidad, and from Isla Mujeres, Yucatán, to Isla de Margarita and Cumana, Venezuela (Figure 124).

Locality records: FLORIDA: Elliot Key, Florida Keys, ocean side; Tortugas (both MCZ). MEXICO: about 3 km N of S tip of Isla Mujeres (RCB); W side of Isla de Cozumel, Yucatán (ANSP). PANAMA: Toro Pt., ocean side (RCB); Cristobal (USNM); Colón (MCZ); Galeta Id.; Ironcastle Pt., Portobelo; Isla Verde, Punta Mantilla, Portobelo (all RCB). COLOMBIA: Santa Marta (MCZ). VENEZUELA: Cumaná (MCZ). BERMUDA: (BMNH). BAHAMA ISLANDS: (numerous records). GREATER ANTILLES: (numerous records). LESSER ANTILLES: (numerous records). BARBADOS: Archers Bay, St. Lucy (RCB). TRINIDAD: rocks W of Bath, Maguaripe Bay (MCZ). CARIBBEAN ISLANDS: *Swan Islands*: (USNM); Great Swan Id. (J. Britton); *Isla de San Andrés*: Johnny Cay; Hansa Club, Paradise Pt. (both RCB, *ex* J. Brooks); *Grand Cayman Island*: (RCB, *ex* J. Brooks); NW point (DMNH); Sand Cay, South West Pt. (ANSP); East End (DMNH); Gun Bay Reef (ANSP, DMNH); Pease Bay, W of Breakers Pt. (ANSP); *Cayman Brac*: South West Pt.; Scott Bay, 1 mi [1.6 km] E of South West Pt. (both ANSP); *Curaçao*: (MCZ); Westpuntbaai; Piscaderabaai; Spaansebaai (all ZMA); *La Blanquilla*: Cabecera (RCB, *ex* C. Franz).

Chiton (*Diochiton*) *squamosus* Species Group

Description: Animal large, reaching 123 mm in length. Central and jugal regions usually smooth; lateral triangle



Explanation of Figures 125 to 127

Shells of *Chiton* (*Diochiton*) *goodallii* Broderip.

Figure 125. Academy Bay, Isla Santa Cruz, Galápagos Ids. (DMNH 43045) (108 mm).

Figure 126. Galápagos Ids., immature specimen that has nodular sculpture (MNHNP) (29.5 mm).

Figure 127. **Holotype** of *Chiton goodallii* Broderip, James Id. [=Isla San Salvador], Galápagos Ids. (BMNH 1951-1-25.12).

not pronounced, rather smooth, or with radiating nodules, which may or may not be offset to form a checkered pattern. Valves flattened and somewhat rounded. Scales with fine sculpture, very small pustules present apically.

Remarks: This group of species includes *Chiton squamosus* Linnaeus from the West Indies, *C. goodallii* Broderip endemic to the Galápagos Islands and Cocos Island, and *C. marquesanus* Pilsbry endemic to the Marquesas Islands. Species of the *C. squamosus* group are among the largest members of the Chitoninae, and *C. goodallii* is certainly the largest. These species differ from the *C. marmoratus* group by their less pronounced lateral triangle and by exhibiting at least an indication of nodes on the lateral triangle, especially in immature examples.

The origin of the *Chiton squamosus* group is not known, but the similarities between these species and the continental New World *Diochiton* strongly suggest that the *C. squamosus* group originated from a New World form, perhaps an ancestor of *C. albolineatus* or *C. articulatus*. Neither *C. goodallii* nor *C. marquesanus* shows any evidence of character release; in spite of their insular existence both species are remarkably constant in shell morphology.

Chiton (*Diochiton*) *squamosus* Linnaeus, 1764

(Figures 94, 101, 109–111, 118, 119)

Chiton squamosum [*sic*] Linnaeus, 1764:465 (in Indiis [herein restricted to Robins Bay, St. Mary, Jamaica]; type in Linnaean Society of London? [not seen]).

Chiton squamosus Linnaeus. Linnaeus, 1767:1107; Thiele, 1893:361, pl. 30, fig. 1 [radula]; Pilsbry, 1893:155, pl. 35, figs. 80–82; Dall & Simpson, 1901:453; Abbott, 1954:325; Abbott, 1958:108; Usticke, 1959:90; Warmke & Abbott, 1961:219, text fig. 33b; de Jong & Kristensen, 1968:29; Kaas, 1972:107, figs. 222–227, pl. 7, fig. 4; Abbott, 1974:405, fig. 4748; Humfrey, 1975:292; Kaas & Van Belle, 1980:123; Lyons, 1981: 38 [distribution in the Bahama Ids.]; Vokes & Vokes, 1983:46, pl. 49, fig. 11; Randall & Martin, 1987:75 [ecology].

Chiton scaber variegatus Chemnitz, 1785:276, pl. 94, figs. 792, 793 [rejected work].

Chiton crassus striatus Chemnitz, 1785:280, pl. 95, fig. 801 [rejected work].

Chiton tigris Spengler, 1797:68 (St. Croix og St. Thomas; type in ZMK).

Chiton striatus Fischer von Waldheim, 1807:112 (reference to Chemnitz [1785:280, pl. 95, fig. 801]; type lost).

Chiton fasciatus Wood, 1815:10, pl. 1, figs. 4, 5 (South America [an error; herein corrected to Robins Bay, St. Mary, Jamaica]; type presumed lost). *Non* Quoy & Gaimard, 1835.

Chiton multimaculatus Blainville, 1825:540 (Port du roi Georges, Nouvelle-Hollande; location of type unknown).

Chiton spengleri Blainville, 1825:538 (location not given; location of type unknown) [*fide* Pilsbry (1894:88)].

Chiton pictus Blainville, 1825:541 (locality unknown; location of type unknown) [*fide* Pilsbry (1894:88)].

Chiton chemnitzii Pfeiffer, 1840:78 ([St. Croix und St. Thomas]; type presumed lost).

Chiton marmoreus (Chemnitz). Reeve, 1847:pl. 12, sp. 64 (Savannah-le-Mer [Haiti], West Indies; type in BMNH). *Non* (Chemnitz) Clessin, 1903 [=*C. marmoratus* Gmelin, 1791].

Chiton (*Lophurus*) *fasciatus* Wood. Shuttleworth, 1853: 198.

Lophyrus fasciatus (Wood). Arango y Molina, 1880:231.

Chiton crassus (Chemnitz). Clessin, 1904:111, pl. 2, fig. 4 (West Indies; location of type unknown).

Description: Medium in size, attaining a length of 55 mm, a width of 40 mm. Valves subcarinate, angle about 95°. Anterior valve convex; post-mucronal slope concave. Mucro rather blunt, anteriorly acentric on posterior valve. Jugal and central regions smooth. Lateral triangle only slightly raised, with five to eight radiating rows of nodules. Surface among these nodules with numerous pits, except for posterior margin on lateral triangle which is smooth. Terminal areas with numerous radiating ribs similar to those on lateral triangle, but nodules sometimes more concentrically arranged. Shell color cream to buff, with dark greenish brown streaks near jugum, lighter, more irregular splotches on central areas. Posterior edges of valves I–VII light orange with one to four black bands. End valves with zigzag markings. Girdle alternately banded light green and white. Interior of shell dull green to blue, posterior depression darker.

Tegmentum: Upper layer of suprategmentum lighter in color; subtegmentum with numerous, rather small canals, not close-packed; jugal subtegmentum reduced somewhat, but present (Figure 119).

Esthete pores: Pores connected by obscure crevices. Megalopores ovate, with slightly beveled edges, three to four times as wide as tear-shaped micropores (Figure 118).

Articulamentum: Central depression of intermediate valves with faint traces of slits; prominent circular slits among ventral grooves of jugal teeth. Primary slit-ray reduced to a field of scattered pores. Secondary slit-ray absent. Insertion teeth deeply pectinate dorsally. Slit formula 11–13/1/13–16.

Girdle scales: Large, rather ovate. Ventro-lateral region granular; apical and dorso-lateral areas with very small pustules (Figure 94).

Radula: Central tooth moderately wide, cup-shaped distally. Pad of centro-lateral teeth elongate, irregular in appearance, and directly attached to tooth. Wing of major lateral nearly rectangular, pointed on one side. Denticle cap rectangular, pointed distally; black tab ovate (Figure 101).

Remarks: *Chiton squamosus* is a distinctive chiton, characterized by its coloration, rounded valves, smooth central areas, and the radial rows of nodules on the lateral triangle and terminal areas. In an eroded condition it is difficult to distinguish from the sympatric *C. marmoratus* Gmelin; examination of the uneroded areas of the valves near the girdle will usually allow identification. Many collections of *C. squamosus* were also observed to include individuals of the sympatric *C. viridis* Spengler. The latter species

differs by: its more sharply raised lateral triangle; relatively smaller girdle scales, which have proportionately larger pustules on the dorso-lateral and apical areas (compare Figures 94, 95); and longitudinal sculpture on the central areas near the lateral triangle. In addition, the larger, more rounded esthete pores differentiate *C. viridis* Spengler (Figure 122) from *C. squamosus* (Figure 118). For a discussion of the confusion between *C. squamosus* and *C. tuberculatus* see remarks under *C. tuberculatus*. The Mediterranean *Rhyssoplax olivacea* (Spengler) was also reported by some authors as *Chiton squamosus*.

It is surprising that this abundant West Indian species has not been the subject of a variety of biological studies. The only paper available that presents ecological information about *Chiton squamosus* was published recently by Randall & Martin (1987) who observed this species along the Caribbean coast of Mexico. Glynn (1970), in his ecological study of *Acanthopleura granulata* (Gmelin) and *C. tuberculatus*, included some notes on the reproductive activity of *C. squamosus*, while Bonnelly *et al.* (1971) reported on the antibiotic properties of its lipids. Ratner (1976:574) investigated the effect of magnetic fields on the radula and shell of "*Chiton squamosis*" [*sic*], but it is likely that he actually was working with *C. tuberculatus*, which is the common species collected "from rocks on the island of Nassau."

Distribution: *Chiton squamosus* occurs from the Bahama Islands south to Grenada in the Lesser Antilles, and along the eastern coast of Yucatán, Mexico (Figure 109). A record from Veracruz is doubtful; no specimens have been seen from any localities in Central America or the northern coast of South America.

Locality records: Mexico: Veracruz (IRSN); Isla Mujeres; Mujeres Harbor (both USNM); about 3 km N of S tip of Isla Mujeres (RCB); Mujeres Harbor (USNM), S end of Isla Mujeres (DMNH); San Miguel, Isla de Cozumel (USNM). Bahama Islands: *Grand Bahama Id.*: Eight Mile Rock (MCZ); *Eleuthera Id.*: (MNHNP); *Cat Id.*: Arthur's Town (MCZ); *San Salvador:* Columbus Pt. (USNM); *Great Inagua*: Matthew Town (DMNH, MCZ). Cay Sal Bank: Elbow Key (MCZ); Anguilla Cay (USNM). Greater Antilles: (numerous records). Lesser Antilles: (numerous records). Caribbean Islands: *Swan Island*: (MCZ, USNM); *Grand Cayman Id.*: Northwest Point (DMNH); *Curaçao*: (RNHL, USNM); Westpuntbaai; Piscaderabaai; Spaansehaven (all ZMA); St. Jorisbaai (MCZ, RCB). *Bonaire*: Porto Spano (ZMA).

Chiton (*Diochiton*) *marquesanus* Pilsbry, 1893

(Figures 100, 105, 109, 116, 117, 120, 121)

Chiton marquesanus Pilsbry, 1893:170, pl. 36, figs. 98–100 (Marquesas Ids.; holotype ANSP 35884); Dupuis, 1918: 527; Dautzenberg & Bouge, 1933:418; Kaas & Van Belle, 1980:81.

Description: Rather large in size, up to 80 mm in length, 45 mm in width. Valves somewhat flattened, angle about 115°. Anterior valve and post-mucronal slope of posterior valve straight. Mucro quite blunt, anteriorly acentric on posterior valve. Jugal and central regions smooth, infrequently exhibiting weak, irregular ribs which bend medially. Lateral triangle not raised, but bordered anteriorly and posteriorly by a radiating rib, between which are four to five radiating rows of irregular, elongate nodules which form a checkered pattern. Shell color greenish black, girdle with light and dark green scales. Interior of shell light bluish green.

Tegmentum: Upper layer of suprategmentum dark; ventral layer lighter in color, with numerous small horizontal canals. Subtegmentum of large, quite close-packed canals with occasional smaller canals above; reduced, but continuous over jugum (Figure 120).

Esthete pores: Megalopores large, round, and 10–12 times as large as round micropores; micropores scattered, few in number (Figure 121).

Articulamentum: Central depression of intermediate valves with scattered slits. Primary slit-ray with oval slits, at times two per longitudinal row. Secondary slit-ray present laterally. Insertion plate deeply pectinate. Slit formula 18/1/22.

Girdle scales: Large, roundly triangular. Ventro-lateral sculpture of rather fine longitudinal ribs which occasionally anastomose, particularly midway to the apex. Apical pustules numerous, very small. Lateral keel evident (Figure 100).

Radula: Central tooth broad, evenly rounded distally, tapering only slightly basally. Pad of centro-lateral conspicuously extended. Wing of major lateral elongate, bluntly pointed distally. Denticle cap attenuate, with conspicuous, elongated black tab (Figure 105).

Remarks: *Chiton marquesanus* is the largest member of the Chitoninae in the Indo-Pacific. It appears to be a rather recent introduction and is certainly a species of New World origin. *Chiton marquesanus* differs from *C. goodallii* Broderip, an endemic Galápagos Island species, by its slightly more arched valves and, above all, by its prominent radial rows of nodules on the lateral triangle which form a checkered pattern. This arrangement is even more prominent on the end valves, and is reminiscent of the sculpture observed in the West Indian *C. tuberculatus* which otherwise differs in having heavily ribbed central areas. Although an immature example of *C. goodallii* may exhibit a similar, but more faint radial sculpture (*fide* specimen in MNHNP; Figure 126), the differences noted warrant specific separation. Both *C. marquesanus* and *C. goodallii* exhibit similar girdle scale and radular morphology. The species differ remarkably in the spatial arrangement of the esthete pores. In *C. marquesanus* the micropores are proportionately smaller and considerably reduced in number (Figure 121). This reduction in the number of micraesthetes was not observed in any New World *Chiton*, but is seen in a number of *Rhyssoplax* species from the Indo-

Pacific region, such as *Rhyssoplax densilirata* (Pilsbry, 1893) and *R. perviridis* (Carpenter, 1865). Thus, it is hypothesized that whatever the function of the micraesthetes, there is reason for certain Indo-Pacific species to have fewer of them.

Chiton marquesanus must be compared with the West Indian *C. squamosus,* in spite of profound color differences, because they have many morphological similarities, including roundly arched valves, completely smooth central areas, blue-green color on the ventral surface of the shell, and nodules on the terminal area. In *C. marquesanus* these nodules are arranged in a checkered pattern; in *C. squamosus* the nodules form radiating rows, which in some cases may be faint. Girdle scale morphology easily differentiates the two species: in *C. squamosus* the scales are flattened and quite rectangular, with very small pustules (Figure 94); in *C. marquesanus* the scales are more roundly triangular and with somewhat larger pustules (Figure 100). As previously mentioned, the esthete pore pattern of *C. marquesanus* is unique among *Chiton* of New World origin and serves to distinguish this species.

A note on a label in the collection of the U.S. National Museum of Natural History states that *Chiton marquesanus* is found "at night on large boulders with algae" and "rare, used as food."

Distribution: *Chiton marquesanus* occurs only in the Marquesas Islands (Figure 109). The species has been reported from Tahiti (Dupuis, 1918; Dautzenberg & Bouge, 1933), but I doubt that it occurs there.

Locality records: Marquesas Islands: (ANSP, IRSN, MNHNP, ZMHU); Eiao (BMNH); Obi Tufa Bay, Eiao (ANSP); Taiohae Bay, Nuku Hiva; Baie de Contrôleur, Nuku Hiva (both USNM); Vai Take Bay, Ua Huka (ANSP); above low tide mark, Atuona Bay, Hiva Oa (ANSP, DMNH).

Chiton (*Diochiton*) *goodallii* Broderip, 1832

(Figures 88, 89, 98, 106, 109, 125, 127)

Chiton goodallii Broderip [*in* Broderip & Sowerby], 1832: 25 (James's Island [=Isla San Salvador], Galápagos Ids.; holotype BMNH 1951.1.25.2); Reeve, 1847:pl. 2, sp. 8; Stearns, 1893:404; Thorpe [*in* Keen], 1971:864, fig. 4.

Chiton godallii [*sic*] Broderip. Sowerby, 1840a:3, figs. 34, 50.

Lophyrus goodallii (Broderip). Carpenter, 1857a:360.

Chiton (*Radsia*) *goodalli* [*sic*] Broderip. Stearns, 1893:449; von Martens, 1902:137; Nierstrasz, 1906:158, figs. 19, 20, 29, 31; Dall, 1909:247; Leloup, 1955:1 [*C. chierchiae* Nierstrasz a junior synonym]; Métivier, 1968: 586 [reported from Santa Elena]; Smith & Ferreira, 1977:89, fig. 13 [reported from the Pleistocene]; Kaas & Van Belle, 1980:54.

Chiton (*Radsia*) *goodallii* Broderip. Pilsbry, 1893:191, pl. 28, figs. 5–8, pl. 29, fig. 9; Boone, 1933:201, pl. 126.

Chiton magnificus "Deshayes" Haller, 1894:28, pl. 2 [misidentification, *fide* Plate (1899)].

Chiton goodalli [*sic*] Broderip. Plate, 1899:67, pl. 4, fig. 192 [anatomy]; Bergenhayn, 1930:29, pl. 8, fig. 72 [shell structure]; Sabelli & Tommasini, 1980:402.

Chiton (*Lophyrus*) *goodalii* [*sic*] Broderip. Clessin, 1903:3, pl. 4, fig. 1.

Chiton (*Radsia*) *chierchiae* Nierstrasz, 1906:158, pl. 3, figs. 15–18, 21–28, 30, 31 (Galápagos Ids.; type in Zoological Museum, Utrecht [not seen]).

Chiton goodalii [*sic*] Broderip. Parker, 1964:151, 166 [erroneously reported from the Gulf of California].

Description: Animal very large, attaining a length of 123 mm, a width of 67 mm. Valves flattened, angle about 120°. Anterior valve convex; post-mucronal slope of posterior valve straight. Mucro blunt, anteriorly acentric on posterior valve. Jugal and central regions smooth. Lateral triangle barely raised, slightly concave, at times with traces of very fine radial ribs. End valves smooth with obsolete to fine, irregular, radial ribs. Shell brown to dark greenish brown. Girdle greenish brown. Interior of shell bluish white, with some reddish brown in central depression and, occasionally, on muscle scars.

Tegmentum: Suprategmentum of moderate thickness; subtegmentum prominent, composed of one to three layers of close-packed canals which vary in size, and which continue over jugum (Figure 89).

Esthete pores: Megalopores large, round, with slightly beveled edges, about four to five times as large as the rather round micropores (Figure 88).

Articulamentum: Central depression of intermediate valves with numerous slits. Each primary slit-ray with a few slits per longitudinal row. Secondary slit-ray present laterally. Insertion teeth deeply pectinate. Slit formula 23/2–3/28.

Girdle scales: Large, roundly triangular. Ventro-lateral sculpture of thin, somewhat irregular ribs which present a granular appearance dorsally. Apical pustules small, quite numerous (Figure 98).

Radula: Central tooth moderately broad, rounded distally, tapering somewhat basally; shaft troughlike. Centrolateral pad clearly visible. Wing of major lateral elongate, pointed distally. Denticle cap attenuate, with distinct elongate tab (Figure 106).

Remarks: The two *Chiton* species which endemically cooccur on the Galápagos Islands, *C. goodallii* and *C. sulcatus* Wood, are the two largest *Chiton* known. No explanation has been offered to account for this phenomenon. *Chiton goodallii* appears to be most closely related to *C. marquesanus* Pilsbry from the Marquesas Islands. The latter species differs by having: low, irregular, radiating nodes on the lateral triangle and terminal areas; a single slit per side on the intermediate valves, not two or three; and light blue on the interior of the shell. *Chiton goodallii* appears more distantly related to the large mainland *C. articulatus* Sowerby and the smaller *C. albolineatus* Broderip & Sowerby (see remarks under these species).

The lateral triangle and end valves of *Chiton goodallii* are generally smooth, as most authors have noted. How-

ever, some examples show faint radiating rows of nodules (SMITH & FERREIRA, 1977). The presence of faint sculptural detail may be especially obvious in some juvenile specimens (Figure 126).

As SMITH & FERREIRA (1977) noted, *Chiton goodallii* is a popular food item among some of the inhabitants of the Galápagos Islands, and piles of shells may be seen in some areas. This is but one example of chitons being utilized as a food source by various people around the world.

The correct spelling of the name must be the original spelling: "*goodallii*" (see remarks under *C. stokesii*).

Distribution: *Chiton goodallii* is known only from the Galápagos Islands and Cocos Island (Figure 109) [for Cocos Id. records, see HERTLEIN (1963)]. The few records in the literature citing *C. goodallii* from Central and South America are highly questionable. This species has been reported from the Pleistocene of the Galápagos Islands (SMITH & FERREIRA, 1977).

Locality records: GALÁPAGOS ISLANDS: (numerous records); *Isla San Cristobal* [Chatham Id.]: (NRS); Wreck Bay [valves only] (ANSP). *Isla Española* [Hood Id.]: (ANSP, ZMK); Isla Gardner, near Isla Española (ANSP). *Isla Santa Maria* [Charles Id.]: (BMNH). *Isla Santa Cruz* [Indefatigable Id.]: on rocks at extreme low tide at Academy Bay (DMNH); Conway Bay (IRSN). *Isla San Salvador* [Santiago or James Id.]: (BMNH). *Isla Isabela* [Albermarle Id.]: in 25 ft [7.6 m] (DMNH); Iguana Cove (ANSP). *Isla Fernandina* [Narborough Id.]: opposite Tagus Cove (ANSP).

Chiton (*Diochiton*) *marmoratus* Species Group

Description: Entire shell smooth; lateral triangle depressed or slightly raised. Valves subcarinate to rounded.

Remarks: This species group includes *Chiton marmoratus* Gmelin from the West Indies and *C. articulatus* Sowerby from the eastern Pacific. Both species must be considered to compose a species pair, and their divergence from a common ancestor probably occurred after the formation of the Panamanian land bridge early in the Pliocene. Of the New World Chitoninae, only the *C. marmoratus* group has closely related species in both the Atlantic and Pacific oceans.

On first glance, *Rhyssoplax fosteri* (Bullock), described by BULLOCK (1972b) as a member of *Chiton s.s.*, looks as if it belongs to the *C. marmoratus* species group. The African species is quite similar to *C. articulatus* in shell form and *C. marmoratus* in color pattern. However, the esthete pore morphology differs significantly from the New World species and the radula is that of *Rhyssoplax*, not *Chiton*.

Chiton (*Diochiton*) *marmoratus* Gmelin, 1791

(Figures 3, 5, 11, 92, 108, 132–135, 137, 139, 142)

Chiton marmoreus CHEMNITZ, 1785:282, pl. 95, figs. 803–805 [rejected work].

Chiton marmoratus GMELIN, 1791:3205, sp. 15 (in Oceano americano; location of type unknown); WOOD, 1825:2, pl. 1, fig. 8; REEVE, 1847:pl. 2, sp. 6; THIELE, 1893: 362, pl. 30, fig. 3 [radula]; PILSBRY, 1893:158, pl. 34, figs. 72–76; DALL & SIMPSON, 1901:454; THIELE, 1910b: 112; ABBOTT, 1954:325; ABBOTT, 1958:108; USTICKE, 1959:90; WARMKE & ABBOTT, 1961:219, text fig. 33e; DE JONG & KRISTENSEN, 1968:29; KAAS, 1972:110, figs. 228–234, pl. 7, fig. 3; ABBOTT, 1974:405, fig. 4749; HUMFREY, 1975:292; HAAS & KRIESTEN, 1978:253 [esthetes]; KAAS & VAN BELLE, 1980:81; LYONS, 1981:38 [distribution in the Bahama Ids.]; BABOOLAL *et al.*, 1981: 40, fig. 3; FERREIRA, 1983:320; VOKES & VOKES, 1983: 46, pl. 49, fig. 9; FERREIRA, 1985:202; RANDALL & MARTIN, 1987:75 [ecology].

Chiton variegatus RÖDING, 1798:196 (no locality given; location of type unknown). *Non* Blainville, 1825, *non* Philippi, 1836.

Chiton scarabaeus REEVE, 1847:pl. 12, sp. 66 (locality unknown; holotype in BMNH).

Chiton (*Lophurus*) *marmoratus* Chemnitz [*sic*]. SHUTTLEWORTH, 1853:198.

Lophyrus marmoratus (Chemnitz) [*sic*]. ARANGO Y MOLINA, 1880:232.

Chiton (*Lophyrus*) *marmoratus* Gmelin. CLESSIN, 1903:10, pl. 6, fig. 5 [not pl. 3, figs. 7–9].

Chiton (*Tonicia*) *marmoreus* (Chemnitz). CLESSIN, 1903:21, pl. 2, fig. 8 (Westindische Inseln; location of type unknown). *Non* Fabricius, 1780, *non* (Chemnitz) Reeve, 1847.

Description: Medium in size, up to 58 mm in length and 32 mm in width. Valves rounded, angle about 95°. Anterior valve convex, post-mucronal slope of posterior valve convex. Mucro moderately blunt, anteriorly acentric on posterior valve. Entire tegmental surface smooth; lateral triangle barely raised. Shell color variable, usually cream with varying dark brown stripes on jugal region and light brown and white zigzag markings on much of each valve (Figure 132). Some specimens very dark brown (Figure 135). Girdle with alternating bands of dark green and light greenish white.

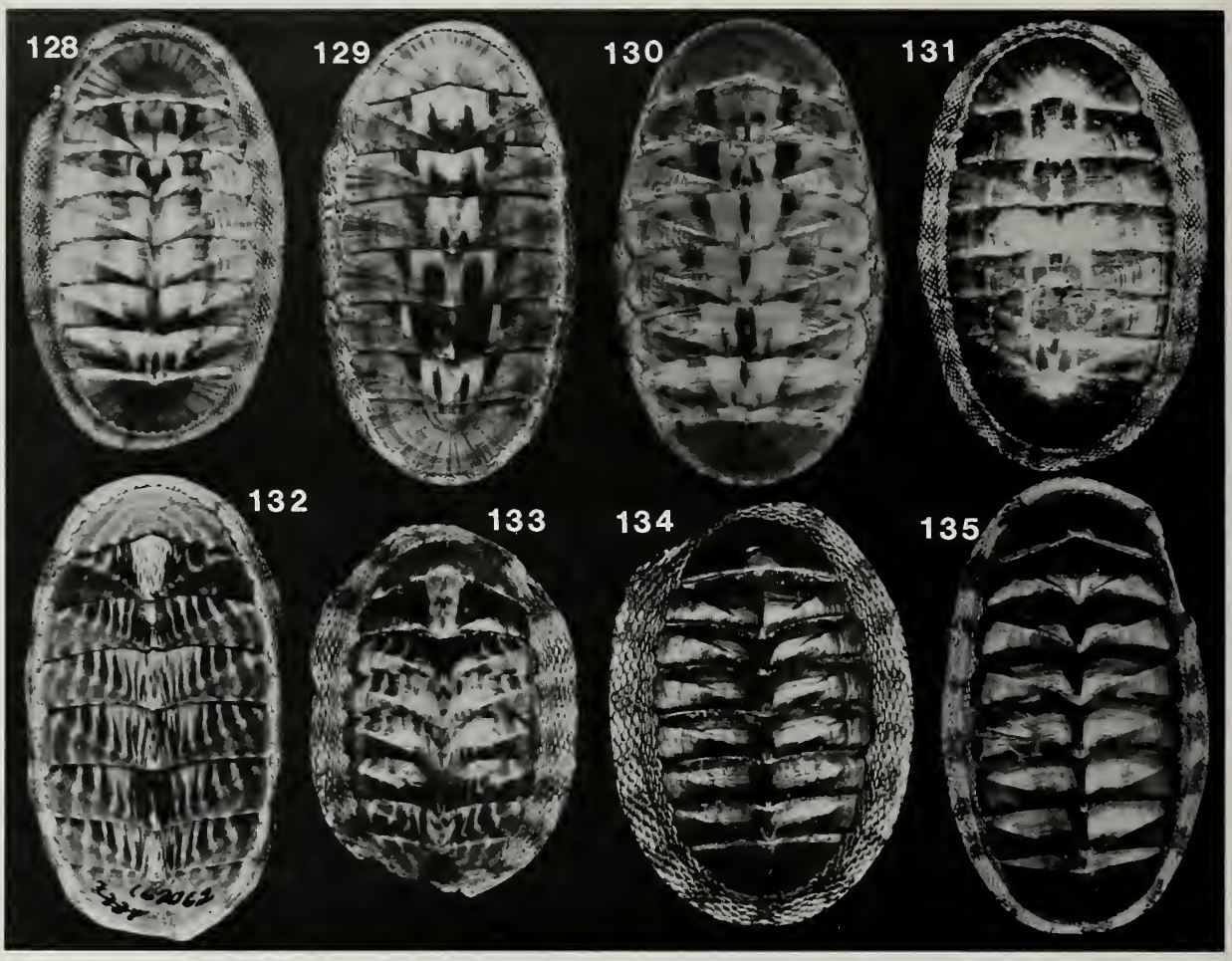
Tegmentum: Upper layer of suprategmentum less porous; subtegmentum with moderately large, non-close-packed canals with smaller canals above, and greatly reduced at jugum (Figure 137).

Esthete pores: Megalopores large, round, with slightly beveled edges, about five to six times as large as round to ovate micropores (Figure 139).

Articulamentum: Central depression with numerous prominent esthete slits in jugal tract. Primary slit-ray with well-developed slits; secondary slit-ray poorly developed. Insertion teeth deeply pectinate. Slit formula 11–15/1/13–19.

Girdle scales: Moderately large, longitudinally ovate. Ventro-lateral areas with extremely fine reticulate sculpture. Apical region with scattered, very small pustules (Figure 92).

Radula: Central tooth moderately broad, deeply cup-shaped and somewhat triangular distally, tapering basally. Pad of centro-lateral conspicuous. Wing of major lateral



Explanation of Figures 128 to 135

Shells of *Chiton* (*Diochiton*) *articulatus* Sowerby and *Chiton* (*Diochiton*) *marmoratus* Gmelin.

Figures 128 and 131. *C.* (*D.*) *articulatus,* Isla Venados, Mazatlán, Mexico (SDSC) (Figure 128, 44 mm; Figure 131, 43.5 mm).

Figure 129. *C.* (*D.*) *articulatus,* locality unknown (BMNH) (41 mm).

Figure 130. *C.* (*D.*) *articulatus,* Acapulco, Mexico (RCB) (39 mm).

Figure 132. *C.* (*D.*) *marmoratus,* Tortugas, Florida (MCZ) (42 mm).

Figure 133. *C.* (*D.*) *marmoratus,* Pelican Cove, St. Croix, Virgin Ids. (RCB) (25.5 mm).

Figure 134. *C.* (*D.*) *marmoratus,* Isla Verde, Punta Mantilla, Portobelo, Panama (RCB) (27.5 mm).

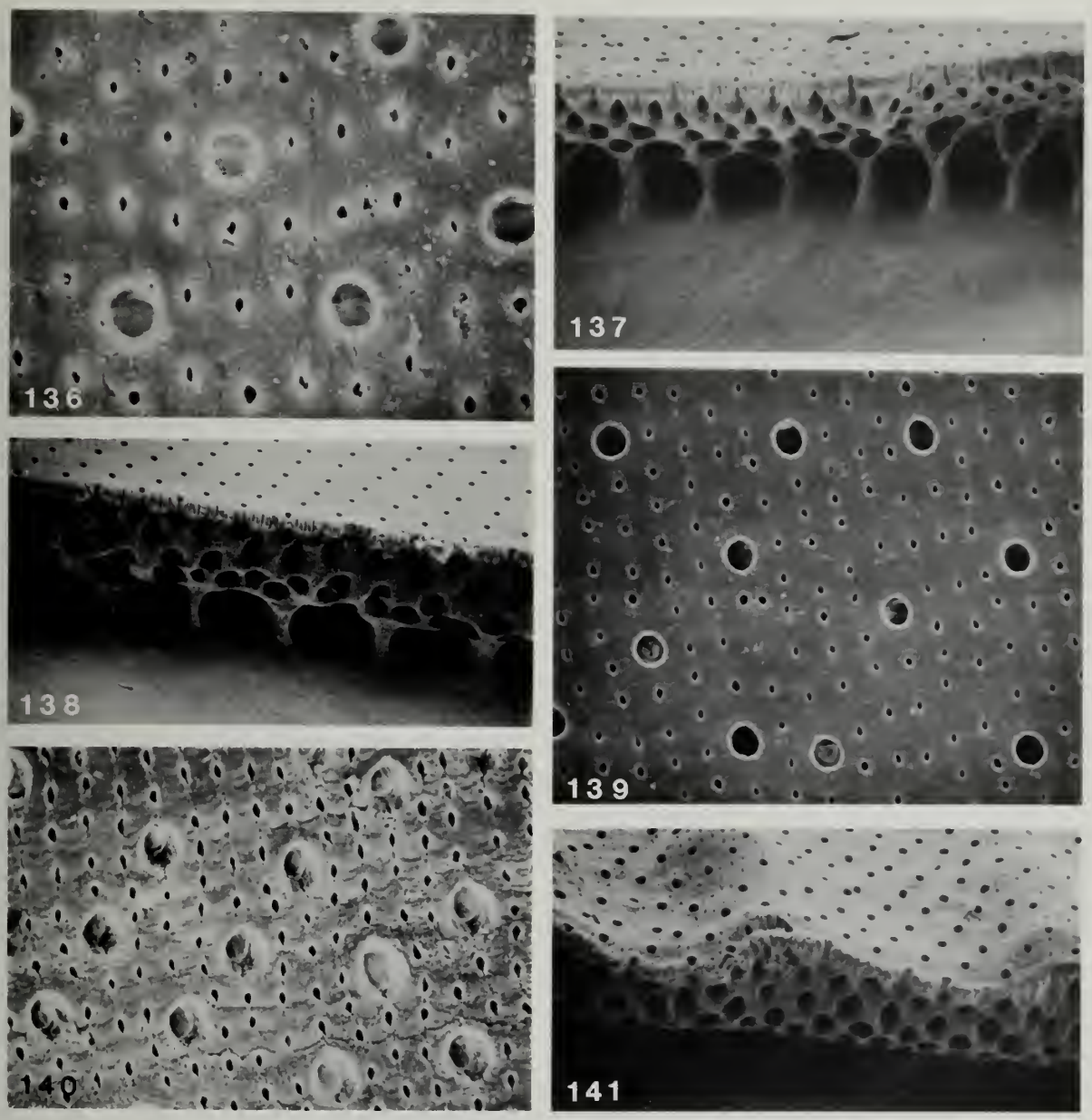
Figure 135. *C.* (*D.*) *marmoratus,* Bridgetown, Barbados (RCB) (43 mm).

rather rectangular, slightly pointed distally. Denticle cap rectangular, barely pointed; tab ovate, not completely surrounded by brown substance (Figures 11, 108).

Remarks: Pilsbry (1893) and Ferreira (1983) noted the obvious close relationship between *Chiton marmoratus* and the Panamic *C. articulatus* Sowerby. The following differences in color and sculpture may be used to distinguish them: *C. marmoratus* lacks the dark blue-green coloration on the muscle scars posterior to the apophyses, often has a more rounded shell, usually has irregular concentric zigzag or even striped markings, the jugal tract and slit-ray consist of numerous prominent slits, the jugal sinus is proportionately wider, and the girdle scales are proportionately larger. The girdle scale morphology of the two species differs sharply. In *C. marmoratus,* the pustules of the dorso-lateral areas are very small, whereas in *C. articulatus* these pustules are quite large, irregularly elongate, and their presence limited to the exposed area of the girdle scale (compare Figures 92 and 93).

Randall & Martin (1987) reported on the existence of three color morphs of *Chiton marmoratus*: light, dark, and reddish. Abbott (1974) had also noted three color groups, but much color variation is seen, and the biological significance of color variation in this, or any other chiton, species is unknown.

Some southern Antillean populations have more angulate valves, approaching *Chiton articulatus* in this respect.



Explanation of Figures 136 to 141

Esthete pores and anterior tegmental innervation of *Chiton* (*Diochiton*) *articulatus* Sowerby, *Chiton* (*Diochiton*) *marmoratus* Gmelin, and *Chiton* (*Chondroplax*) *granosus* Frembly.

Figures 136 and 138. *C.* (*D.*) *articulatus,* Acapulco, Mexico (RCB) (Figure 136, ×594; Figure 138, ×85).

Figures 137 and 139. *C.* (*D.*) *marmoratus,* Isla Verde, Punta Mantilla, Portobelo, Panama (RCB) (Figure 137, ×85; Figure 139, ×339).

Figures 140 and 141. *C.* (*Chondroplax*) *granosus,* locality unknown (ZMK) (Figure 140, ×339; Figure 141, ×85).

Specimens from Trinidad (in MCZ) exhibit the exterior coloration of *C. articulatus,* but the articulamental structures clearly place these specimens in *C. marmoratus.*

Distribution: *Chiton marmoratus* is found from the Bahama Islands and throughout the West Indies to Trinidad, and from Isla Mujeres, Yucatán, to the north coast of Venezuela (Figure 142). The record from Veracruz, Mexico, appears doubtful. Although ABBOTT (1974) reported this species to be "rare at Key Biscayne," I have seen no specimens from southern Florida. In spite of some labels that state "Bermuda" [see below], it appears likely that *C. marmoratus* does not occur there, as FERREIRA (1985) noted. JENSEN & HARASEWYCH (1986) in their report on Bermudian mollusks did not list this species.

Locality records: MEXICO: Veracruz (IRSN); Isla Mujeres (ANSP, USNM); E shore, about 2 mi [3.2 km] S of

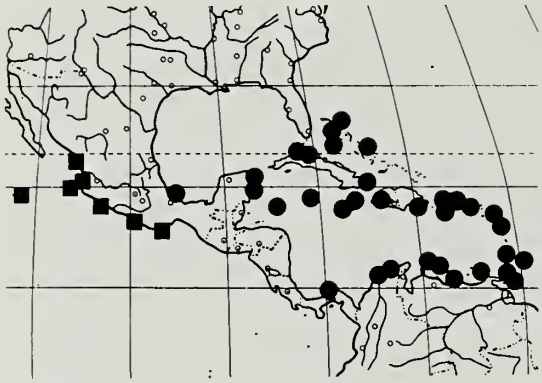


Figure 142

Distribution of *Chiton* (*Diochiton*) *articulatus* Sowerby (■) and *Chiton* (*Diochiton*) *marmoratus* Gmelin (●).

N end, Isla Mujeres (ANSP); Mujeres Harbor (USNM); about 3 km N of S tip, Isla Mujeres (RCB); W side, Isla de Cozumel (ANSP); San Miguel, Isla de Cozumel (USNM). PANAMA: Toro Pt., ocean side (RCB); Colon (MCZ); Ft. Randolph (USNM); Isla Verde, Punta Mantilla, Portobelo (RCB). COLOMBIA: vicinity of Cartagena (USNM); Cartagena; Galera Zamba, near Cartagena (both ANSP); Santa Marta (IRSN, NRS, USNM); rock point, N end of Rodadero Beach, Santa Marta (ANSP). VENEZUELA: Borborata, Maraven, E of Puerto Cabello (RCB, *ex* Martins); La Guaira (IRSN, RNHL, ZMHU); Isla de Margarita (MNHNP); Playa de Agua, 1 mi [1.6 km] N of Cabo Blanco, Isla de Margarita (MCZ); just N of La Guardia, Isla de Margarita (RCB, *ex* C. Franz). BERMUDA: (NMB, MCZ, USNM). BAHAMA ISLANDS: *Great Abaco*: E coast, N end of Elbow Cay (ANSP); *New Providence*: Gambier (ANSP); *Andros Id.*: E of Morgan's Bluff (MCZ); *San Salvador*: Columbus Pt. (USNM); *Exuma Id.*: Black Pt. (ANSP). GREATER ANTILLES: (numerous records). LESSER ANTILLES: (numerous records). BARBADOS: (numerous records); off the castle, E Barbados (USNM); Bathsheba (ANSP); Bridgetown (RCB). TRINIDAD: (MCZ; RCB, *ex* Bacon; USNM); rocks W of Bath, Maguaripe Bay (MCZ); Maguaripe Beach (RCB); Maracas Bay (RNHL). CARIBBEAN ISLANDS: *Swan Id.*: (MCZ); *Grand Cayman Id.*: Jackson Pt. (ANSP); *Cayman Brac*: Southwest Pt.; Scott Bay, 1 mi [1.6 km] E of Southwest Pt. (both ANSP); *Curaçao*: (RNHL, USNM, ZMA); Westpuntbaai (ZMA); Port Marie (RCB); Piscaderabaai (RCB, ZMA); St. Michaelsbaai (RNHL); Caracasbaai (RNHL, ZMA); Spaansebaai, Spaansehaven; Spaansewater (all ZMA); SW pt. of Tobago, S coast (RNHL); Boca La Cadera (ZMA); St. Jorisbaai (MCZ, RCB); *Bonaire*: (MCZ).

Chiton (*Diochiton*) *articulatus* Sowerby, 1832

(Figures 4, 93, 107, 128–130, 136, 138, 142)

Chiton laevigatus Sowerby [*in* BRODERIP & SOWERBY], 1832: 59 (Guaymas [Gulf of California]; type in BMNH? [not found]); REEVE, 1847:pl. 7, sp. 35; PILSBRY, 1893: 159, pl. 34, figs. 68–71; PILSBRY & LOWE, 1932:130; ABBOTT, 1954:325. *Non* Fleming, 1813.

Chiton articulatus Sowerby [*in* BRODERIP & SOWERBY], 1832: 59 (St. Blas [Gulf of California]; type in BMNH? [not found]); REEVE, 1847:pl. 4, sp. 7; DALL, 1879:79, 125, pl. 3, fig. 22 [radula]; KEEN, 1958:517, fig. 2; Thorpe [*in* KEEN], 1971:864, fig. 3; ABBOTT, 1974:405, fig. 4750; KAAS & VAN BELLE, 1980:10; FERREIRA, 1983:319, figs. 6, 24, 25, 26.

Lophyrus articulatus (Sowerby). CARPENTER, 1857a:317; CARPENTER, 1857b:190.

Chiton (*Lophyrus*) *laevigatus* Sowerby. CLESSIN, 1903:6, pl. 5, fig. 3.

Chiton (*Lophyrus*) *articulatus* Sowerby. CLESSIN, 1903:13, pl. 7, fig. 4.

Chiton similis [Gray MS], *fide* specimen label in Gray collection, BMNH.

Description: Animal large, up to 104 mm in length, 59 mm in width. Angle of valves about 105°. Anterior valve and post-mucronal region of posterior valve convex. Mucro obsolete, anteriorly acentric on posterior valve. Entire surface of shell smooth; lateral triangle barely raised. Shell color off-white to yellowish or olive green; lateral triangles yellowish brown to bluish green, occasionally with a few darker concentric bands. Jugal and central regions with longitudinal streaks of dark brown. Interior of shell white to light yellowish white; central depression and callus greenish, with characteristic dark green on anterior muscle scars and, at times, on jugal teeth. Girdle alternately banded light and dark green.

Tegmentum: Upper layer of suprategmentum lighter in color, thin and less porous; subtegmentum composed of a few irregular layers of close-packed, medium-sized canals, and continuous over jugum (Figure 138).

Esthete pores: Megalopores large, round, with slightly beveled edges, five to seven times as large as more slitlike, ovate micropores (Figure 136).

Articulamentum: Jugal tract with small number of scattered slits, mature examples with more elongate, close-packed slits. Secondary slit-ray present. Insertion teeth deeply pectinate. Slit formula 13–18/1/16–22.

Girdle scales: Moderate in size, somewhat glossy. Ventro-lateral areas seemingly smooth; distally very fine, irregularly granular ribs present. Primary sculpture consisting of large pustules and irregularly elongate nodules which are restricted to distal portion of scale except for an acute triangular portion which medially extends basally (Figure 93).

Radula: Central teeth moderately narrow, rounded distally, tapering basally. Wing of major lateral teeth broad, somewhat pointed distally. Denticle cap shovel-like, nearly rounded distally, but flattened a little medially; tab ovate, completely surrounded by brown substance (Figure 107).

Remarks: *Chiton articulatus* is morphologically most similar to the West Indian *C. marmoratus* Gmelin with which it has been confused (see remarks under that species). The large *C. goodallii* Broderip, endemic to the Galápagos Islands, may have arisen from an ancestor of *C. articulatus*.

Chiton goodallii differs by being larger, flatter, lacking the blue-green muscle scars posterior to the apophyses, having a dark brown shell, and having proportionately larger girdle scales. In addition, the insertion plate of the intermediate valves of *C. goodallii* consistently has more than a single slit per side. The girdle scales of the two species are very different.

Thorpe (*in* KEEN, 1971) and FERREIRA (1983) placed *Lophyrus striatosquamosus* Carpenter, 1857, as a junior synonym of *C. articulatus*. I have not examined the unique type specimen, which is in the British Museum (Natural History), and I am therefore not able to corroborate Thorpe's conclusion. Carpenter's original figures, which were published by BRANN (1966), and the photograph in KEEN (1968:pl. 59, fig. 91) are of little help in determining the identity of Carpenter's species. The smoothness of the shell and the pectination of the insertion teeth are similar to a young *C. articulatus,* but the striated girdle scales indicate still another species. KEEN (1968:433) reported that "the girdle is not preserved." The systematic status of Carpenter's *L. striatosquamosus* remains questionable.

Distribution: *Chiton articulatus* occurs from Mazatlán, Mexico, south to Puerto Guatulco, Mexico. The record from Guaymas is doubtful (Figure 142).

Locality records: MEXICO: Guaymas (ZMHU); E side of Isla Venados, NW of Mazatlán; S of Punta Chile, W of Mazatlán (both ANSP); Mazatlán (numerous records); Mendia (USNM); San Blas (ANSP, MNHNP, USNM); Islas Tres Marias (ANSP, IRSN, MCZ); Bahía de Santiago, 10 mi [16.1 km] N of Manzanillo (USNM); Manzanillo (DMNH, ZMK); Acapulco (ANSP, MCZ, MNHNP, RCB); Puerto Guatulco (ZMK).

Subgenus *Chondroplax* Thiele, 1893

Chondroplax THIELE, 1893:363. Type species, designated by VAN BELLE (1983), *Chiton granosus* Frembly, 1827.

Description: Animal medium in size, reaching 75 mm in length, valves flattened. Jugal tract smooth, central areas with somewhat beaded longitudinal ribs. Lateral triangle and terminal areas with radial rows of nodules. Interior of valves white with dull blue muscle scars. Central depression with long, close-packed, transverse grooves. Girdle scales roundly triangular; ventro-lateral sculpture of irregular, longitudinal, granular ribs. Denticle cap of radula elongate, unicuspidate. Central tooth very broad, with narrow base.

Remarks: *Chondroplax* differs from all other subgenera of *Chiton* by its large, rounded nodules on the terminal areas. For the most part, the radula also distinguishes *Chondroplax*; the extremely broad central tooth and flaring centro-lateral teeth are not found elsewhere in *Chiton* except in *Chiton* (*Chiton*) *stokesii* Broderip. When compared with other chitons, *Chondroplax* resembles only *Sypharochiton*. Both groups have rather heavy shells, but the widely spaced nodules on the terminal areas of *Chondroplax* serve to differentiate the two groups. Also, the denticle cap of the major lateral tooth of *Chondroplax* is elongate and unicuspidate (Figure 130), and the central tooth is very broad. In *Sypharochiton* the denticle cap is shovel-like, at times with evidence of a secondary cusp on each side of the main cusp, and the central tooth is only moderately broad (BULLOCK, 1988). *Radsia* is differentiated from *Chondroplax* by its radial ribs or rows of close-packed nodules of the lateral triangle, and the denticle cap, which is not as elongate and has a reduced secondary cusp (BULLOCK, 1988).

THIELE (1893) included two nominal species in *Chondroplax*: *Chiton granosus* Frembly and *Chiton stockesi* [*sic*] Broderip. The former was designated by VAN BELLE (1983) as the type species of the genus; the latter "species," a misidentification, was in fact also *Chiton granosus* Frembly (*fide* THIELE, 1909).

Chiton (*Chondroplax*) *granosus* Frembly, 1827

(Figures 96, 97, 103, 140, 141, 143, 144)

Chiton granosus FREMBLY, 1827:200, suppl. pl. 17, fig. 1 (Valparaiso; location of type unknown); REEVE, 1847: pl. 5, sp. 27; PILSBRY, 1893:167, pl. 30, figs. 27, 28; PLATE, 1899:56, pl. 4, fig. 190 [anatomy]; DALL, 1909: 247; BERGENHAYN, 1930:pl. 7, fig. 67 [shell structure]; MARINCOVICH, 1973:43, fig. 98; KAAS & VAN BELLE, 1980:77; OTAÍZA & SANTELICES, 1985:229–240 [vertical distribution].

Lophyrus granosus (Frembly). TAPPARONE-CANEFRI, 1874: 75.

Gymnoplax ludoviciae ROCHEBRUNE, 1884:38 (Nouvelle Calédonie [error; herein designated as Valparaiso, Chile]; syntype in IRSN); PILSBRY, 1894:100 [translation of original description].

Chondroplax granosa (Frembly). THIELE, 1893:364, pl. 30, fig. 8 [radula].

Chondroplax stockesi "Broderip" THIELE, 1893:364 [spelling error and misidentification, *fide* THIELE (1909)].

Chiton (*Chondroplax*) *granosus* Frembly. THIELE, 1909:2; THIELE, 1929:20, fig. 11 [radula].

Chiton ludoviciae (Rochebrune). THIELE, 1910a:94, pl. 10, figs. 12–15 [type figured]; KAAS & VAN BELLE, 1980: 77.

Description: Animal medium in size, up to 75 mm in length, 55 mm in width. Angle of rather flat, often eroded valves about 100°. Anterior valve convex; post-mucronal slope straight. Mucro moderately blunt; centrally located on posterior valve. Jugal tract smooth, central areas with somewhat beaded longitudinal ribs. Lateral triangle barely raised; low, broad, nodular rib extends along diagonal line. Often a few other radiating rows of nodules appear on lateral triangle. Terminal areas with 10–12 radiating rows of widely spaced nodules. Color of tegmentum nearly totally dark brown to greenish brown, with occasional streaks of cream white on jugal and central areas. Girdle black. Interior of valves white with dull blue muscle scars and reddish brown on posterior slope of callus.

Tegmentum: Suprategmentum extending over subteg-

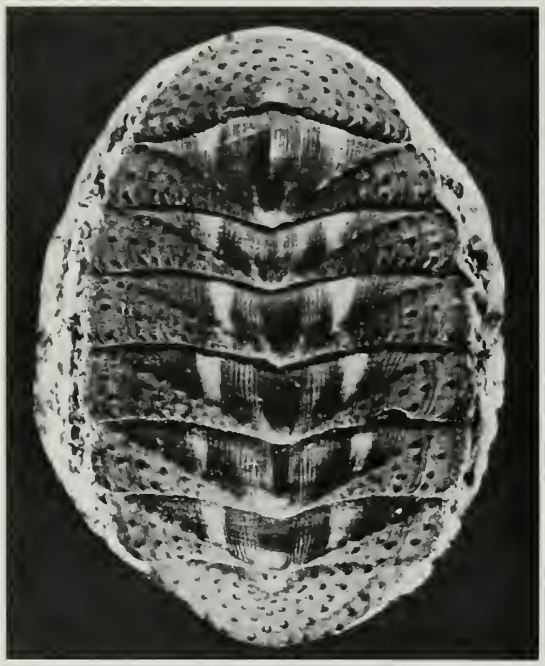


Figure 143

Shell of *Chiton* (*Chondroplax*) *granosus* Frembly, Valparaiso, Chile, girdle scales lacking (USNM 19299a) (30.5 mm).

Figure 144

Distribution of *Chiton* (*Chondroplax*) *granosus* Frembly.

mentum at anterior edge of intermediate valve, becoming thinner toward jugum. Ventral portion of suprategmentum with numerous, moderately close-packed, rather small, horizontal canals. Subtegmentum of varying sized, close-packed canals, becoming thinner at jugum, but not obsolete (Figure 141).

Esthete pores: Megalopores large, round to ovate, with conspicuously beveled edges, eight to nine times as wide as ovate micropores which are often connected by obscure crevices (Figure 140).

Articulamentum: Central depression of intermediate valve broad; esthete slits located within extremely numerous, long, close-packed, transverse grooves which extend laterally to insertion teeth. Primary slit-ray composed of longitudinal slits near insertion teeth, numerous close-packed holes in posterior depression. Secondary slit-ray present as region of small holes. Lateral portions of muscle scars and entire posterior slope of callus with numerous small holes. Insertion teeth deeply pectinate. Slit formula 12/1/14–15.

Girdle scales: Roundly triangular; entire lateral surface quite irregular; ventro-lateral sculpture of non-close-packed series of granules and granular ribs arranged longitudinally. Apical area rough, somewhat granular. Base often with granular ribs; no basal depression (Figures 96, 97).

Radula: Central tooth large, broad, quite flat distally, tapering slightly toward base. Basal portion of centro-lateral tooth greatly extended; no evidence of centro-lateral pad, although slight extension of lateral edge is evident. Wing of major lateral broad, very conspicuous. Denticle cap rather attenuate; tab moderately elongate; magnetite encloses tab except for small area laterally. Tan substance restricted to thin band on lateral side, a thicker band medially (Figure 103).

Remarks: *Chiton granosus* is easily differentiated from *Sypharochiton pelliserpentis* (Quoy & Gaimard), with which it could possibly be confused, by its large, widely separated nodes on the terminal areas, and by the radula, which has a simple, broad central tooth with a narrow base, and a denticle cap that is unicuspidate, lacking any indication of secondary cusps. *Chiton* (*Chondroplax*) *granosus* differs also by having numerous, transverse, close-packed grooves in the central depression which extend not just within jugal tract, but across the valve.

This common Chilean chiton appears to occupy a niche similar to that of *Acanthopleura*. When this species was described, Frembly (1827:201) noted:

> "This new species is found plentifully at Valparaiso in the fissures of the rocks, but generally out of the reach of the breakers: the habits of this species are very different from those of the others which have come under my observation: like many *Patellae* they are sometimes at such a distance from the water as would lead one to suppose that they pass some considerable part of their existence apart from it."

The biology of *Chiton granosus* is poorly known. According to Moreno & Jaramillo (1983), *C. granosus*

feeds principally on barnacle larvae. At Mehuín, Chile, *C. granosus* attains a density of 20 individuals/m^2 and the chiton serves as prey for the muricid gastropod *Concholepas concholepas* (Bruguière) and the seagull *Larus dominicanus* (JARA & MORENO, 1984). In an investigation on the vertical distribution of chitons in central Chile, OTAÍZA & SANTELICES (1985) reported that *Chiton granosus* is the "most abundant species of chiton on the rocky intertidal habitats studied." According to these authors, the species attains its greatest density in the mid intertidal zone on steep rock walls; the smallest individuals were observed within beds of the mussel *Perumytilus purpuratus* (Lamarck, 1819). MARINCOVITCH (1973) collected numerous examples at Iquique, Chile, "on undersides of rocks, lower intertidal zone."

Based on examination of syntypes, Rochebrune's *Gymnoplax ludoviciae* is conspecific with *Chiton granosus* and the former, which has not been recognized previously, can be removed from the list of species occurring in New Caledonia.

Distribution: *Chiton* (*Chondroplax*) *granosus* ranges from northern Peru south to Isla de Chiloé, Chile (Figure 144).

Locality records: PERU: Tumbes (ZMHU); Salaverry; Ancón (both USNM); Callao (ZMHU); Isla San Lorenzo, off Callao (IRSN, MCZ); Lima (ZMHU); Chorrillos, S of Lima (DMNH); Bahía Paracas (MCZ); Matarani (ZMK); Mollendo (MCZ, USNM). CHILE: Arica (RNHL, USNM); Junín (NRS); Iquique (numerous records); Cavanha Beach, Iquique (USNM); Mejillones (MCZ); Cruz Grande (USNM); Coquimbo (BMNH); Los Vilos (ANSP, DMNH); near Papudo, N of Valparaiso (MCZ); Torpederas, near Valparaiso (USNM); Valparaiso (numerous records); Talcahuano (MCZ, RNHL); off Lota (MCZ); Puerto Montt (ZMHU); Calbuco (RNHL); San Pedro, Isla de Chiloé (MCZ).

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LITERATURE CITED

ABBOTT, R. T. 1954. American seashells. D. Van Nostrand Co.: New York. 541 pp., 40 pls.

ABBOTT, R. T. 1958. The marine mollusks of Grand Cayman Island, British West Indies. Monogr. Acad. Natur. Sci. Philadelphia. No. 11:138 pp., 5 pls.

ABBOTT, R. T. 1974. American seashells. 2nd ed. Van Nostrand Reinhold Co.: New York. 663 pp., 24 pls.

ADAMS, C. B. 1845. Specierum novarum conchyliorum, in Jamaica repertorum, synopsis. Proc. Boston Soc. Natur. Hist. 2:1–17.

ADAMS, C. B. 1852. Catalogue of shells collected at Panama, with notes on their synonymy, station, and geographical distribution. R. Craighead: New York. 335 pp. [Ann. Lyceum Natur. Hist. New York 5:225–560.]

ADAMS, H. & A. ADAMS. 1853–1854. The genera of Recent Mollusca 1. J. Van Voorst: London. 484 pp. [Family Chitonidae, pp. 467–484, July 1854.]

ALLAN, J. 1959. Australian shells. Revised ed. Georgian House: Melbourne. 487 pp.

ANGAS, G. F. 1867. A list of species of marine Mollusca found in Port Jackson Harbour, New South Wales, and on the adjacent coasts, with notes on their habits, &c. Part I. Proc. Zool. Soc. London for 1867:185–233.

ARANGO Y MOLINA, R. 1878–1880. Contribución a la fauna malacológica Cubana. G. Montiel y Comp.: Habana. Pp. 1–24 [1878], pp. 25–136 [1879], 137–280 [1880].

AREY, L. B. & W. J. CROZIER. 1919. The sensory responses of *Chiton*. Jour. Exper. Zool. 29:157–260.

BABOOLAL, S., S. JOHNATTY & Z. ALI. 1981. Studies on the Trinidad chitons. Living World, J. Trinidad and Tobago Field Nat. Club 1981–82:39–45.

BARNES, D. W. 1824. Descriptions of five species of *Chiton*. Amer. Jour. Sci. Art 7:69–71, pl. 3.

BERGENHAYN, J. R. M. 1930. Kurze Bemerkungen zur Kenntnis der Schalenstruktur und Systematik der Loricaten. K. Svenska Vetenskapsakademiens Handl. (3)9(3):3–54, pls. 1–10.

BLAINVILLE, H. DE. 1825. Oscabrion, *Chiton*. Dictionnaire des Sciences Naturelles 36:519–556.

BONNELLY, I., N. NUNEZ, S. JAKOWSKA, J. PEREZ, E. LEBRON & E. CONTRERAS. 1971. Antibiotic properties of the lipid fraction of *Chiton squamosus* from the Caribbean coast of the Dominican Republic. Amer. Zool. 11:520.

BOONE, L. 1933. Scientific results of cruises of the yachts "Eagle" and "Ara," 1921–1928, William K. Vanderbilt, commanding. Coelenterata, Echinodermata and Mollusca. Bull. Vanderbilt Marine Mus. 4:217 pp., 133 pls.

BOREHAM, A. 1959. Biological type specimens in the New Zealand Geological Survey. I. Recent Mollusca. New Zealand Geol. Survey, Paleont. Bull. No. 30:87 pp.

BRANN, D. C. 1966. Illustrations to "Catalogue of the collection of Mazatlan shells" by Philip P. Carpenter. Paleontol. Res. Inst.: Ithaca. 111 pp., 60 pls.

BRODERIP, W. J. & G. B. SOWERBY. 1832–1833. Characters of new species of Mollusca and Conchifera collected by Mr. Cuming. Proc. Committee of Science and Correspondence of the Zoological Society of London for 1832:25–33, 50–61, 104–108, 113–120, 124–126 [all 1832]; 173–179, 194–202 [both 1833].

BULLOCK, R. C. 1972a. On the taxonomy of *Chaetopleura fulva* (Wood 1815) (Mollusca: Polyplacophora). Occasional Papers on Mollusks, Mus. Comp. Zool., Harvard Univ. 3:177–191, pls. 33–35.

BULLOCK, R. C. 1972b. Notes on the genus *Chiton* in the western Indian Ocean (Mollusca: Polyplacophora). Occasional Papers on Mollusks, Mus. Comp. Zool., Harvard Univ. 3:237–251, pls. 43, 44.

BULLOCK, R. C. 1985. The *Stenoplax limaciformis* (Sowerby, 1832) species complex in the New World (Mollusca: Polyplacophora: Ischnochitonidae). Veliger 27:291–307, 24 figs.

BULLOCK, R. C. 1988. The systematics of the Southern Hemisphere chiton genera *Radsia* Gray, 1847, and *Sypharochiton* Thiele, 1893 (Mollusca: Polyplacophora: Chitonidae). Proc. Biol. Soc. Washington 101:280–299.

BULLOCK, R. C. & K. J. BOSS. 1971. *Lithophaga aristata* in the shell-plates of chitons (Mollusca). Breviora, Mus. Comp. Zool. No. 369:10 pp., 8 figs.

CARPENTER, P. P. 1857a. Report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Rept. British Assoc. Adv. Sci. for 1856:159–368, pls. 6–9.

CARPENTER, P. P. 1857b. Catalogue of the Reigen collection of Mazatlan Mollusca, in the British Museum. Warrington. 552 pp.

CHEMNITZ, J. H. 1785. Anmerkungen zum Geschlechte der vielschalichten Napfmuscheln, welche mit sichtbaren Gelenken versehen sind und beym Linné Chitones heissen. *In:* Martini & Chemnitz, Systematisches Conchylien-Cabinet 8: 252–293, pls. 94–96.

CHEMNITZ, J. H. 1788. Nachlese aus dem Geschlechte der Chitonen odor vielschalichten Napfmuscheln. *In:* Martini & Chemnitz, Systematisches Conchylien-Cabinet 10:370–376, pl. 173 [in part].

CLENCH, W. J. & R. D. TURNER. 1950. The western Atlantic marine mollusks described by C. B. Adams. Occasional Papers on Mollusks, Mus. Comp. Zool., Harvard 1:233–403, pls. 29–49.

CLESSIN, S. 1903–1904. Die Familie Chitonidae. *In:* Martini & Chemnitz, Systematisches Conchylien-Cabinet 6(4):pls. 1–3 [1843]; pls. 4–15 [1902]; pp. 1–96, pls. 16–39 [1903]; pp. 97–135, pls. 40, 41 [1904].

COWDEN, R. 1961. A cytochemical investigation of oögenesis and development to the swimming larval stage in the chiton *Chiton tuberculatum* [*sic*] L. Biol. Bull. 120:313–325.

COWDEN, R. 1963. Some histochemical observations on the foot of *Chiton tuberculatum* [*sic*] L. Trans. Amer. Microsc. Soc. 82:406–416, 13 figs.

COWDEN, R. 1974. Fluorescence cytochemical studies on oocyte growth in *Chiton tuberculatum* [*sic*], with special emphasis on protein end-group methods. Differentiation 2:249–255.

COX, L. R. 1958. Question of the name to be used for the class typified by the genus "*Chiton*" Linnaeus, 1758. Bull. Zool. Nomencl. 15:543–546.

CROZIER, W. J. 1918. Growth and duration of life of *Chiton tuberculatus*. Proc. Natur. Acad. Sci. 4:322–325.

CROZIER, W. J. 1919a. Coalescence of the shell-plates in *Chiton*. Amer. Natur. 53:278–279.

CROZIER, W. J. 1919b. Growth of *Chiton tuberculatus* in different environments. Proc. Natl. Acad. Sci. 5:325–328.

CROZIER, W. J. 1920. Note on the photic sensitivity of the chitons. Amer. Natur. 54:376–380.

CROZIER, W. J. & L. B. AREY. 1918. On the significance of the reaction to shading in *Chiton*. Amer. Jour. Physiol. 46: 487–492.

CROZIER, W. J. & L. B. AREY. 1920. On the ethology of *Chiton tuberculatus*. Proc. Natl. Acad. Sci. 5:496–498.

CRUZ, R. A. & A. SOTELA. 1984. Contribución a la biología de *Chiton stockesii* [*sic*] (Polyplacophora: Chitonidae) de Punta Pochote, Puntarenas, Costa Rica. Rev. Biol. Trop. 32: 61–68.

DALL, W. H. 1879. Report on the limpets and chitons of the Alaskan and Arctic regions, with descriptions of genera and species believed to be new. Proc. U.S. Natl. Mus. 1:281–344, pls. 1–5 [Sci. Results Expl. Alaska: art. 4, pp. 63–126].

DALL, W. H. 1909. Report on a collection of shells from Peru, with a summary of the littoral marine Mollusca of the Peruvian zoological province. Proc. U.S. Natl. Mus. 37(1704): 147–294, pls. 20–28.

DALL, W. H. & C. T. SIMPSON. 1901. The Mollusca of Porto Rico. Bull. U.S. Fish Comm. for 1900:351–524, pls. 53–58.

DANCE, S. P. 1966. Shell collecting: an illustrated history. Faber and Faber: London. 344 pp.

DAUTZENBERG, PH. & J.-L. BOUGE. 1933. Les mollusques testacés marins des établissements français de l'Océanie. Jour. de Conchyl. 77:41–469.

DAVIS, G., R. ROBERTSON & M. MILLER. 1979. Catalog of the chiton types of the Academy of Natural Sciences of Philadelphia. Tryonia, No. 1:1–60.

DESHAYES, G. P. 1827. Oscabrion. *Chiton*. Dictionnaire Classique d'Histoire Naturelle 12:446–457.

DESHAYES, G. P. 1836. Oscabrion (*Chiton*). *In:* Lamarck, His-

toire naturelle des animaux sans vertèbres. 2nd ed. 7:482–520.

DODGE, H. 1952. A historical review of the mollusks of Linnaeus. Part 1. The classes Loricata and Pelecypoda. Bull. Amer. Mus. Natur. Hist. 100(1):1–263.

DUPUIS, P. 1918. Notes concernant les polyplacophores (suite). Bull. Mus. Hist. Natur. Paris 24:525–533.

EMERSON, W. K. & W. E. OLD, JR. 1964. Additional records from Cocos Island. Nautilus 77:90–92.

FERREIRA, A. J. 1978. The chiton species described by C. B. Adams, 1845, from Jamaica. Bull. Mar. Sci. 28:81–91.

FERREIRA, A. J. 1983. The chiton fauna of the Revillagigedo Archipelago, Mexico. Veliger 25:307–322, 10 text-figs.

FERREIRA, A. J. 1985. Chiton (Mollusca: Polyplacophora) fauna of Barbados, West Indies, with the description of a new species. Bull. Mar. Sci. 36:189–219.

FERREIRA, A. J. 1986. A revision of the genus *Acanthopleura* Guilding, 1829 (Mollusca: Polyplacophora). Veliger 28:221–279.

FISCHER, P.-H. 1978. L'habitat littoral parmi les mollusques polyplacophores. Jour. de Conchyl. 115:30–55.

FISCHER VON WALDHEIM, G. 1807. Muséum-Demidoff, ou catalogue systématique et raissonné des curiosités de la nature et de l'art, 3. Université Imperiale: Moscow. 330 pp., 6 pls.

FREMBLY, J. 1827. A description of several new species of chitones, found on the coast of Chili, in 1825; with a few remarks on the method of taking and preserving them. Zool. Jour. 3:193–205, suppl. pls. 16, 17.

GLYNN, P. 1968. Ecological studies on the associations of chitons in Puerto Rico, with special references to sphaeromid isopods. Bull. Mar. Sci. 18:572–626.

GLYNN, P. 1970. On the ecology of Caribbean chitons *Acanthopleura granulata* Gmelin and *Chiton tuberculatus* Linne: density, mortality, feeding, reproduction, and growth. Smithsonian Contributions to Zoology, No. 66:21 pp.

GMELIN, J. F. 1791. Caroli a Linné Systema naturae per regna tria naturae. 13th ed. 1(6):3021–3910. Lipsiae.

GRAY, J. E. 1828. Spicilegia Zoologica; or original figures and short systematic descriptions of new and unfigured animals. Part I, 7 pp., pls. 1–6.

GRAY, J. E. 1847a. On the genera of the family Chitonidae. Proc. Zool. Soc. London for 1847:63–70.

GRAY, J. E. 1847b. Additional observations on chitones. Proc. Zool. Soc. London for 1847:126–127.

HAAS, W. & K. KRIESTEN. 1978. Die Astheten mit intrapigmentären Schalenauge von *Chiton marmoratus* L. (Mollusca, Placophora). Zoomorphologie 90:253–268.

HADDON, A. 1886. Report on the Polyplacophora collected by H.M.S. Challenger during the years 1873–76. Repts. Scient. Results Voyage Challenger 15(43):50 pp., 3 pls.

HALLER, B. 1882–1883. Die Organisation der Chitonen der Adria, I. Arbeiten aus dem Zoologischen Institut der Universität Wien und der Zoologischen Station in Triest 4:323–396, 8 pls. [1882]; II. *Ibid.* 5:29–60, 3 pls. [1883].

HALLER, B. 1894. Beiträge zur Kenntnis der Placophoren. Morph. Jahrb. 21:28–39, pl. 2.

HERRMANNSEN, A. N. 1846–1847. Indicis Generum Malacozoorum Primordia 1. T. Fischeri: Cassellis. 637 pp. [Suppl. 1852.]

HERTLEIN. 1963. Contribution to the biogeography of Cocos Island, including a bibliography. Proc. Calif. Acad. Sci. (4)32: 219–289.

HÖGLUND, N. & F. RAHEMTULLA. 1977. The isolation and characterization of acid mucopolysaccharides of *Chiton tuberculatus*. Comp. Biochem. Physiol. 56B:211–214.

HUMFREY, M. 1975. Sea shells of the West Indies. Taplinger: New York. 351 pp., 32 pls.

HUTTON, F. W. 1880. Manual of the New Zealand Mollusca. Hughes: Wellington. 224 pp.

HUTTON, F. W. 1882. Notes on some branchiate Gastropoda. Trans. New Zealand Inst., 1882, 15:118–131, pls. 13–16.

HUTTON, R. F., B. ELDRED, K. D. WOODBURN & R. M. INGLE. 1956. The ecology of Boca Ciega Bay with special reference to dredging and filling operations. Florida State Board of Conservation Marine Laboratory, Tech. Ser. No. 17:87 pp.

INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE [ICZN]. 3rd ed. 1985. Univ. California Press: Berkeley. 338 pp.

IREDALE, T. 1914. The chiton fauna of the Kermadec Islands. Proc. Malacol. Soc. London 11:25–51.

IREDALE, T. 1915. A commentary on Suter's "Manual of the New Zealand Mollusca." Trans. New Zealand Inst. 47:417–497.

IREDALE, T. & A. F. B. HULL. 1926. A monograph of the Australian loricates. VI. Australian Zool. 4:164–185, pls. 18–20; VII. *Ibid.* 4:256–276, pls. 37–39.

IREDALE, T. & A. F. B. HULL. 1927. A monograph of the Australian loricates. Sydney and Melbourne: Sydney. 168 pp., 21 pls.

IREDALE, T. & A. F. B. HULL. 1932. The loricates of the Neozelanic region [continued]. Australian Zool. 7:119–164, pls. 7–10.

JARA, H. F. & C. A. MORENO. 1984. Herbivory and structure in a midlittoral rocky community: a case in southern Chile. Ecology 65:28–38.

JENSEN, R. H. & M. G. HARASEWYCH. 1986. Class Polyplacophora. Pp. 394–397. *In:* W. Sterrer (ed.), Marine fauna and flora of Bermuda: a systematic guide to the identification of marine organisms. John Wiley & Sons: New York. 742 pp.

JONG, K. M. DE & I. KRISTENSEN. 1968. Gegevens over de Mollusken van Curaçao, utigezonderd de mariene Gastropoden. Correspond. Nederlandse Malacol. Vereniging, Suppl. 1968, 45 pp., 4 pls.

KAAS, P. 1972. Polyplacophora of the Caribbean region. Studies Fauna Curaçao 41(137):1–162, 9 pls., numerous text-figs.

KAAS, P. & R. A. VAN BELLE. 1980. Catalogue of living chitons. W. Backhuys: Rotterdam. 144 pp.

KEEN, A. M. 1958. Sea shells of tropical west America. Stanford Univ. Press: Stanford. 619 pp.

KEEN, A. M. 1968. West American types at the British Museum (Natural History) IV. Carpenter's Mazatlan collection. Veliger 10:389–439, pls. 55–59.

KEEN, A. M. 1971. Sea shells of tropical west America. 2nd ed. Stanford Univ. Press: Stanford. 1064 pp., 22 pls. [Class Polyplacophora, pp. 861–882, by S. Thorpe.]

KIND, C. & R. MEIGS. 1955. Sterols of marine mollusks. IV. Δ^7-cholestenol, the principal sterol of *Chiton tuberculatus* L. Org. Chem. 20:1116–1118.

KING, P. O. 1832. Description of the Cirrhipeda, Conchifera and Mollusca, in a collection formed by the officers of H.M.S. Adventure and Beagle employed between the years 1826 and 1830 in surveying the southern coasts of South America, including the Straits of Magalhaens and the coast of Tierra del Fuego. Zool. Jour. 5:332–349.

KNOX, G. A. 1963. Problems of speciation in intertidal animals with special reference to New Zealand shores. Pp. 7–29. *In:* J. P. Harding & N. Tebble (eds.), Speciation in the sea. Systematics Association Publ. No. 5. The Systematics As-

sociation: London. [Includes remarks on chiton ecology from P. M. Johns, 1960, unpubl. M.Sc. thesis, Univ. of Canterbury.]

LAWRENCE, J. M. 1970. The lipid composition of the organs of two species of tropical chitons. Caribbean Jour. Sci. 10: 1–3.

LELOUP, E. 1955. *Chiton* (*Radsia*) *goodalli* Broderip, 1832 = *Chiton* (*Radsia*) *chierchiae* Nierstrasz, 1908. Bull. Hist. Roy. Sci. Natur. Belgique 31(23):10 pp., figs.

LELOUP, E. 1956. Reports of the Lund University Chile Expedition 1948–1949. 27. Polyplacophora. Lunds Universitets Årsskrift, N.F., Avd. 2, Bd. 52, Nr. 15. 94 pp.

LEWIS, J. B. 1960. The fauna of rocky shores of Barbados, West Indies. Canadian Jour. Zool. 38:391–435.

LINNAEUS, C. 1758. Systema naturae. 10th ed. 1. L. Salvii: Holmiae. 824 pp.

LINNAEUS, C. 1764. Museum s:ae r:ae m:tis Ludovicae Ulricae reginae Svecorum. Holmiae. 720 pp. [Reference not seen.]

LINNAEUS, C. 1767. Systema naturae. 12th ed. 1(2). L. Salvii: Holmiae. Pp. 531–1364.

LOWE, R. T. 1825. Descriptions of some shells belonging principally to the genus *Chiton*. Zool. Jour. 2:93–108.

LOWENSTAM, H. 1962. Magnetite in denticle capping in Recent chitons (Polyplacophora). Bull. Geol. Soc. Amer. 73:435–438, 1 pl.

LOWENSTAM, H. 1967. Lepidocrocite, an apatite mineral and magnetite in teeth of chitons (Polyplacophora). Science 156: 1373–1375, 3 figs.

LYONS, W. G. 1981. Comments on chitons (Mollusca: Polyplacophora) of the Bahama Islands. Bull. Amer. Malacol. Union for 1981:38–39.

MARINCOVITCH, L. 1973. Intertidal mollusks of Iquique, Chile. Bull. Los Angeles County Mus. Natur. Hist. 16:1–49, 102 figs.

MARTENS, E. VON. 1902. Die Meeres-Conchylien der Cocos-Insel. SitzungsBericht der Gesellschaft Naturforschender Freunde zu Berlin for 1902:137–141.

MAY, W. L. 1921. A checklist of the Mollusca of Tasmania. J. Vail: Hobart. 114 pp.

MAY, W. L. 1923. An illustrated index of Tasmanian shells. J. Vail: Hobart. 100 pp.

MENZIES, R. J. & P. W. GLYNN. 1968. The common marine isopod Crustacea of Puerto Rico. A handbook for marine biologists. Studies Fauna Curaçao 27:1–133.

METCALF, M. 1892. Preliminary notes upon the embryology of *Chiton*. Johns Hopkins Univ. Circular 11:79–80.

METCALF, M. 1893. Contributions to the embryology of *Chiton*. Studies Biol. Lab., Johns Hopkins Univ. 5:249–267.

MÉTIVIER, B. 1968. Mollusques marins récoltés par M. R. Hoffstetter sur les côtes de l'équateur et aux Iles Galápagos. Chitonidae et Fissurellidae. Bull. Mus. Natl. Hist. Natur. (2)40:585–596.

MEUSCHEN, F. C. 1787. Museum Geversianum, sive index rerum naturalitum . . . comparavit A. Gevers publice distrahendam. Rotterdam.

MORENO, C. A. & E. JARAMILLO. 1983. The role of grazers in the zonation of intertidal macroalgae of the Chilean coast. Oikos 41:73–76.

MORRIS, P. 1973. A field guide to shells of the Atlantic and Gulf coasts and the West Indies. Houghton Mifflin: Boston. 330 pp., 76 pls.

NEAVE, S. A. 1940. Nomenclator zoologicus 4. R. Clay: London. 758 pp.

NIERSTRASZ, H. 1905a. Die Chitonen der Siboga-Expedition. Siboga-Expeditie 20(48):114 pp., 8 pls.

NIERSTRASZ, H. 1905b. Bemerkungen ueber die Chitonen-Sammlung im Zoologischen Museum zu Leiden. Notes from the Leyden Museum 25:141–159, pls. 9, 10.

NIERSTRASZ, H. F. 1906. Remarks on the Chitonidae. Tijdschrift der Nederlandsche Dierkundige Vereeniging (2)10: 141–172, pl. 3.

OLSSON, A. A. 1961. Mollusks of the tropical eastern Pacific. Panamic-Pacific Pelecypoda. Norton: Ithaca. 575 pp., 86 pls.

OTAÍZA, R. D. & B. SANTELICES. 1985. Vertical distribution of chitons (Mollusca: Polyplacophora) in the rocky intertidal zone of central Chile. Jour. Exp. Mar. Biol. Ecol. 86:229–240.

PAETEL, F. 1875. Die bisher veröffentlichten Familien- und Gattungsnamen der Mollusken. Gebrüder Paetel: Berlin. 229 pp.

PARKER, R. H. 1964. Zoogeography and ecology of some macroinvertebrates, particularly mollusks, in the Gulf of California and the continental slope off Mexico. Vidensk. Medd. fra Dansk Naturh. Foren. 126:1–178, pls. 1–15.

PETIT DE LA SAUSSAYE, S. 1856. Deuxième supplément au catalogue des coquilles trouvées à la Guadeloupe. Jour. de Conchyl. 5:149–158.

PFEIFFER, L. 1840. Kritisches Register zu Martini und Chemnitz's Systematisches Konchylien-Kabinet. T. Fischer: Kassel. 112 pp.

PILSBRY, H. A. 1892–1894. Polyplacophora. Manual of conchology. Vol. 14:1–128, pls. 1–30 [1892]; 129–350, pls. 31–68 [1893]. Vol. 15:1–64, pls. 1–10 [1893]; 65–132, pls. 11–17 [1894].

PILSBRY, H. A. & H. N. LOWE. 1932. West Mexican and Central American mollusks collected by H. N. Lowe, 1929–31. Proc. Acad. Natur. Sci. Philadelphia 84:33–144, 17 pls.

PLATE, L. 1897–1902. Die Anatomie und Phylogenie der Chitonen. Zoologische Jahrbücher, Suppl. Vol. 4 [Fauna Chilensis 1]:1–243, pls. 1–12 [1897]. Vol. 5 [Fauna Chilensis 2]:15–216, pls. 2–11 [1899]; 281–592, pls. 12–16 [1901].

QUOY, J. R. C. & J. P. GAIMARD. 1835. Mollusques. Voyage de l'Astrolabe (Zool.) 3:1–644, 93 pls.

RANDALL, C. W. & R. F. MARTIN. 1987. Distribution, abundance, and movement patterns of shoreline chitons of the Caribbean coast of Mexico. Nautilus 101:75–79.

RATNER, S. C. 1976. Kinetic movements in magnetic fields of chitons with ferro-magnetic structures. Behavioral Biology 17:573–578.

REEVE, L. 1847. Monograph of the genus *Chiton*. Conchologia Iconica 4:33 pls.

REHDER, H. A. 1932. [*Chiton miltoplax.*] Pl. 10, figs. 4, 5 [figures only—nude name].

RIGHI, G. 1968. On the radulae and spines of some Polyplacophora and Archeogastropoda from Curaçao. Studies Fauna Curaçao 25:73–82.

ROCHEBRUNE, A. T. DE. 1884. Diagnoses d'espèces nouvelles de la famille des Chitonidae (deuxième supplément). Bull. Soc. Philomathique Paris (7)8:32–39.

RÖDING, P. F. 1798. Museum Boltenianum. Trappii: Hamburg. 199 pp.

ROMASHKO, S. 1984. The shell book. 5th ed. Windward Publ.: Miami. 64 pp.

SABELLI, B. & S. TOMMASINI. 1982 [1980]. I Molluschii marini raccolti dalla Spedizione "L. Mares—G.R.S.T.S." alle Isole Galápagos. 2. Polyplacophora. Pp. 401–410. *In:* Museo Zoologico dell'Università di Firenze, "L. Mares—G.R.S.T.S." Gruppo Ricerche Scientifiche e Tecniche Subacquee. Firenze: 426 pp. [Published as a separate in April 1980.]

SALISBURY, A. E. 1953. Mollusca of the University of Oxford

Expedition to the Cayman Islands in 1938. Proc. Malacol. Soc. London 30:39–54, pls. 7, 8.

SAMPSON, L. V. 1895. The musculature of *Chiton*. Jour. Morphol. 11:595–628, pls. 31–33.

SCHMIDT-EFFING, U. 1980. Beobachtungen zum Heimfinde-Verhalten und zum Aktivitäts-Rhythmus von *Chiton stokesii* Broderip, 1832 mit Anmerkungen auch zu *Ischnochiton dispar* (Sowerby, 1832) (Polyplacophora). Zoologischer Anzeiger, Jena 205:309–317.

SHUTTLEWORTH, R. J. 1853. Über den Bau der Chitoniden, mit Aufzählung der die Antillen und die Canarishen Inseln bewohnenden Arten. Mittheilungen der naturforschenden Gesellschaft in Bern, 1853:169–207. [Reprinted separately in Diagnosen neuer Mollusken, No. 4:45–83.]

SMITH, A. G. 1960. Amphineura. *In:* R. C. Moore, Treatise on invertebrate paleontology, Part I, Mollusca 1:41–86, figs. 31–45.

SMITH, A. G. & A. J. FERREIRA. 1977. Chiton fauna of the Galápagos Islands. Veliger 20:82–97, 4 pls.

SMITH, A. G., N. F. SOHL & E. L. YOCHELSON. 1968. New Upper Cretaceous Amphineura (Mollusca). Geol. Survey Prof. Paper 593-G:9 pp., 1pl.

SMITH, M. 1937. East coast marine shells. Edwards Brothers: Ann Arbor. 308 pp., 74 pls.

SOLEM, A. 1972. Malacological applications of scanning electron microscopy.—II. Radular structure and functioning. Veliger 14:327–336, 6 pls.

SOUTHWICK, W. E. 1939. The "agglutination" phenomenon with spermatozoa of *Chiton tuberculatus*. Biol. Bull. 77:157–165.

SOWERBY, G. B. 1825. A catalogue of the shells contained in the collection of the late Earl of Tankerville. Sowerby: London. 92 pp., 9 pls.

SOWERBY, G. B. 1840a. A catalogue of the Recent species of chitons. *In:* Conchological illustrations. Sowerby: London. 10 pp.

SOWERBY, G. B. 1840b. Descriptions of some new chitons. Charlesworth's Mag. Natur. Hist. 4:287–294.

SPENGLER, L. 1797. Udforlig Beskrivelse ovet det mangeskallede Konkylie-Slaegt of Linneus Kaldet *Chiton*. Skrivter af Naturhistorie-Selskabet 4:62–103, pl. 6.

STEARNS, R. E. C. 1893. Scientific results of explorations by the U.S. Fish Commission Steamer Albatross. XXV.—Report on the mollusk-fauna of the Galápagos Islands, with descriptions of new species. Proc. U.S. Natl. Mus. 16:353–450, pls. 51–52.

STEPHENSON, T. A. & A. STEPHENSON. 1972. Life between tidemarks on rocky shores. W. H. Freeman and Company: San Francisco. 425 pp.

SUTER, H. 1897. Revision of the New Zealand Polyplacophora. Proc. Malacol. Soc. London 2:183–201.

SUTER, H. 1899. New Zealand Polyplacophora: keys to genera and species. Trans. Proc. New Zealand Inst. 31:59–64.

SUTER, H. 1905. Supplement to the revision of the New Zealand Polyplacophora, with descriptions of a new species. Jour. Malacol. 12:65–71, pl. 9.

SYKES, J. E. & J. R. HALL. 1970. Comparative distribution of mollusks in dredged and undredged portions of an estuary, with a systematic list of species. Fishery Bulletin 68:299–306.

TAKI, Is. 1962. A list of the Polyplacophora from Japanese Islands and vicinity. Venus 22:29–53.

TAKI, Iw. 1964. Classification of the class Polyplacophora, with a list of Japanese chitons. Venus 22:401–414.

TAPPARONE-CANEFRI, C. 1874. Zoologia del Viaggio Intorno al Globo della Regia Fregata Magenta durante gli Anni 1865–68. Malacologia (Gastropodi, Acefali e Brachiopodi). Paravia: Torino. 161 pp., 4 pls.

THIELE, J. 1893. Polyplacophoren. *In:* F. H. Troschel, Das Gebiss der Schnecken 2:353–401, pls. 30–32.

THIELE, J. 1909–1910. Revision des Systems der Chitonen (I). Zoologica 22:1–58, pls. 1–6 [1909]; (II) 71–132, pls. 7–10 [1910a].

THIELE, J. 1910b. Molluskenfauna Westindiens. Zoologische Jahrbücher, Suppl. 2:109–132, pl. 1.

THIELE, J. 1929. Handbuch der systematischen Weichtierkunde 1. G. Fischer: Jena. 376 pp.

TOMLINSON, J. T. 1959. Magnetic properties of chiton radulae. Veliger 2:36.

USTICKE, G. W. NOWELL-. 1959. A checklist of the marine shells of St. Croix. Lane Press: Burlington. 90 pp., 4 pls.

USTICKE, G. W. NOWELL-. 1969. A supplementary listing of new shells (illustrated). Livingston: Wynnewood, PA. 32 pp., 6 pls.

USTICKE, G. W. NOWELL-. 1971. A supplementary listing of new shells (illustrated) (revised edition). Livingston: Wynnewood, PA.

VAN BELLE, R. A. 1978. Sur la classification des Polyplacophora: V. Classification systématique des Chitonidae (Neoloricata: Chitonina). Informations de la Société Belge de Malacologie, Serie 6, No. 1, pp. 19–28, pl. 8.

VAN BELLE, R. A. 1983. The systematic classification of the chitons (Mollusca: Polyplacophora). Informations de la Société Belge de Malacologie, Serie 11, Nos. 1–3, pp. 1–178.

VOKES, H. E. & E. H. VOKES. 1983. Distribution of shallow-water marine Mollusca, Yucatan Peninsula, Mexico. Mesoamerican Ecology Institute, Monogr. 1 [Middle American Research Institute Publ. No. 54]. Tulane Univ.: New Orleans. 183 pp., 50 pls.

WARMKE, G. & R. T. ABBOTT. 1961. Caribbean seashells. Livingston: Narberth. 346 pp., 44 pls.

WOOD, W. 1815. General conchology. J. Booth: London. 246 pp., 59 pls.

WOOD, W. 1825. Index Testaceologicus. Taylor: London. 212 pp., 38 pls.

WOOD, W. 1828. Supplement to the Index Testaceologicus. Taylor: London. 59 pp., 8 pls.

YAKOVLEVA, A. M. 1952. Pantsyrnye mollyuski morei SSSR [Shell-bearing mollusks (Loricata) of the seas of the USSR]. Izdatel'stvo Akademii Nauk SSSR. 107 pp., 11 pls. [English translation, 1965, Smithsonian-NSF Israel Program for Scientific Translations.]

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Feeding Biology of *Ocenebra lurida* (Prosobranchia: Muricacea): Diet, Predator-Prey Size Relations, and Attack Behavior

by

A. RICHARD PALMER

Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2E9 and
Bamfield Marine Station, Bamfield, British Columbia V0R 1B0, Canada

Abstract. Field observations on individuals from an unusually dense intertidal population of *Ocenebra lurida* (Middendorff, 1849) revealed several interesting features about the feeding biology of this rather enigmatic predatory neogastropod. (1) Unlike the more common drilling gastropods in the northeastern Pacific, *O. lurida* preyed most heavily upon limpets: of 231 feeding observations, 55.0% were limpets (*Lottia pelta* [=*Collisella pelta*], *L. strigatella* [=*C. strigatella*], and *Tectura scutum* [=*Notoacmea scutum*]), 42.0% were barnacles (*Balanus glandula, B. crenatus, Semibalanus cariosus,* and *Chthamalus dalli*), 2.2% were mussels (*Mytilus edulis*), and 0.8% were other prey (*Calliostoma ligatum* and *Spirorbis* sp.). (2) The mean size of both limpets and barnacles consumed increased with increasing predator size, although this increase was not significant statistically for barnacles. (3) Over a broad range of predator size, both the mean and the maximum shell length of eaten *T. scutum* exceeded that of *L. pelta* (by 7 and 5 mm respectively). This observed difference in maximum shell length corresponded rather closely to that expected if the limit to vulnerability were determined by shell thickness, but it could also have resulted from differences in food value between the two species. (4) As observed for the Australian *Dicathais aegrota,* the distribution of drill sites on limpet shells was distinctly nonrandom: 85% of 124 drill holes were located in the posterior half of the limpet's shell and 95% were medial to the pedal retractor muscle scar. (5) When eating limpets, *O. lurida* tended to consume the gonad first, followed by the digestive gland and then the foot, but the foot was eaten only when the shell length of the limpets was less than that of *O. lurida*. (6) When feeding on the barnacle *Semibalanus cariosus, O. lurida* attacked lateral wall plates almost exclusively (37 of 38) and nearly half of the attacks (46%) occurred at the sutures between adjacent plates. Because sutures form only about 15% of the periphery, these results suggest a preference for sutural attack. (7) Patterns in the degree of completion of unfinished drill holes suggest that larger *O. lurida* attack limpets sooner after tidal immersion than smaller ones.

INTRODUCTION

Depending on the taxonomic authority, from four to six species of the cosmopolitan neogastropod genus *Ocenebra* occur along the shores of the northeastern Pacific (Kozloff, 1987): *O. interfossa* Carpenter, 1864, *O. lurida* (Middendorff, 1849), *O. orpheus* (Gould, 1829), *O. painei* (Dall, 1903), *O. sclera* (Dall, 1919), and the introduced *O. japonica* (Dunker, 1869). According to Radwin & D'Attilio (1976), however, *O. sclera* is a synonym of *O. lurida* and *O. japonica* is actually *Ceratostoma inornatum* (Récluz, 1851). Because some species are pests, much of the knowledge of the feeding biology of *Ocenebra* derives from studies of species in commercial oyster beds (Barry, 1981; Chapman & Banner, 1949; Chew & Eisler, 1958; Hancock, 1960). Two species of *Ocenebra* have also been studied under more natural conditions: *O. poulsoni* from California (Fotheringham, 1971) and *O. lumaria* from Japan (Luckens, 1970a, b). Information on the biology of species from the northeastern Pacific, however, is scarce and consists either of anecdotal observations (geographic range, shell color variation, and an unusual mode of feeding in *O. lurida*; Talmadge, 1975) or circumscribed data collected as part of a larger study (feeding and growth in the laboratory, and notes on natural densities of *O. interfossa* and *O. lurida*; Spight *et al.*, 1974). In addition, although prey items have been reported for various *Ocenebra* species worldwide, most of these reports consist of laboratory or

anecdotal observations; hence, remarkably little is known about the normal feeding biology of species in this cosmopolitan genus.

MATERIALS AND METHODS

Most of the field observations were obtained from an unusually dense intertidal population of *Ocenebra lurida* (approx. 1–3/m^2) on the east side of Turn Island, San Juan Islands, Washington (U.S.A.; 48°32′10″N, 122°58′10″W). These observations were made during low tides on five different dates from 1 April to 12 May 1978 (1 IV, 2 IV, 7 V, 10 V, 12 V). A few additional feeding observations were also recorded from Tatoosh Island, Washington (48°19′N, 124°40′W) on 29–30 July 1978. The habitat at Turn Island consisted of a heterogeneous assemblage of rocks and boulders interspersed with bedrock promontories. Most feeding observations were obtained from the lower shore (−0.5 to +0.5 m, U.S. datum). Within this tidal range the rock surfaces were rather barren. Macroalgae were virtually absent, and barnacles were sparse and nearly all roughly one year old or less based on size (<10 mm basal diameter) and lack of weathering on the skeletal plates. Limpets were the most conspicuous invertebrates.

The shell lengths (apex to tip of siphonal canal to 0.1 mm) of both feeding and nonfeeding snails were recorded as well as the number of mating pairs observed on most dates. If a snail was feeding, the size and identity of its prey were also noted. Prey size was measured with Vernier calipers to 0.1 mm as follows: limpets—shell length and shell width; barnacles—anteroposterior opercular diameter inside the parietal plates; mussels—maximum shell length.

Many but not all prey items observed being attacked were collected and taken to the laboratory to determine more precisely the location of attack, the extent of tissue eaten, and, for limpets, the degree of completion and size of the drill hole. The percentage completion of unfinished drill attacks was estimated by eye as a percentage of the shell which had been penetrated at the site of attack. Both maximum and minimum outer drill hole diameters in the limpet shells were measured under a dissecting microscope using a calibrated ocular micrometer. For both of the commonly consumed species of limpets, average diameter (mean of maximum and minimum diameters) of completed drill holes correlated highly with *Ocenebra lurida* shell length (Figure 1; $r^2 = 0.88$; $n = 52$). Using this regression, predator size was estimated for a sample of drilled, dead shells collected at the time of the feeding observations. The only other predatory gastropods observed in the immediate vicinity were the buccinid *Searlesia dira* and the thaidid *Thais emarginata* (=*Nucella emarginata*). Because buccinids are not known to drill (TAYLOR *et al.*, 1980), and *T. emarginata* eats limpets only extremely rarely (see discussion), *O. lurida* was most likely responsible for the drill holes in these dead limpet shells. Furthermore, because of their circular to subcircular outline and nearly parallel sides in the upper half, these holes would not have been made by octopus.

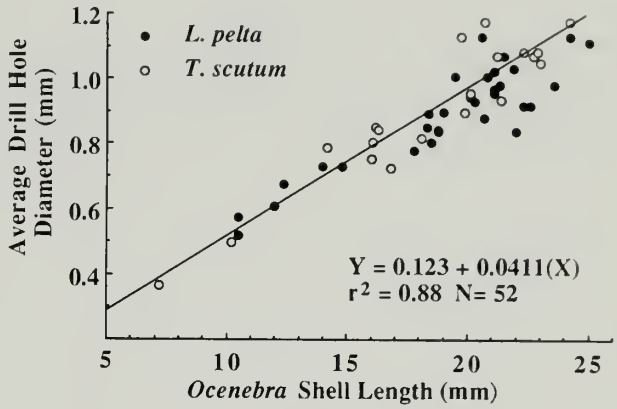

Figure 1

Average outer diameter of drill hole ([max. diam. + min. diam.]/2) as a function of *Ocenebra lurida* shell length for two species of limpets, *Lottia pelta* and *Tectura scutum*.

Statistical analyses were conducted using the microcomputer routines in Statview 512+® (Version 1.0, Abacas Concepts, Berkeley, CA, U.S.A.) except for the analysis of covariance (ANCOVA) and multi-way contingency table analyses which were conducted with BMDP Statistical Software (programs 1V and 4F respectively; DIXON, 1983).

RESULTS

Activity and Diet

At Turn Island, from 59 to 103 *Ocenebra lurida* were observed per day when the feeding observations were made. With one exception, on each date the majority of snails found were in the process of feeding (mean percent feeding = 61% ± 12.4 SD, n = 5 dates, range = 44–75%), and no significant difference in shell length existed either among dates ($P = 0.54$), or between those feeding and those not feeding on a particular date ($P = 0.34$ between activities; two-way ANOVA).

A total of 241 prey items from 11 species of prey were observed in the diet (Table 1). At Turn Island, *Ocenebra lurida* preyed predominantly upon limpets (55.0%), almost exclusively *Tectura scutum* (Rathke, 1833) (=*Notoacmea scutum*) and *Lottia pelta* (Rathke, 1833) (=*Collisella pelta*) (following the nomenclature of LINDBERG [1986]). Barnacles of four species formed the second most common component of the diet (42.0%; primarily *Semibalanus cariosus* (Pallas, 1788) and *Balanus glandula* Darwin, 1854, but also *B. crenatus* Brugière, 1789, and *Chthamalus dalli* Pilsbry, 1916). Mussels (*Mytilus edulis* L.), *Calliostoma ligatum* (Gould, 1849), and *Spirorbis* sp. were eaten only occasionally. Although no quantitative observations were made of actual prey availability at this site, the proportions of prey eaten appeared to be representative of the proportions available on the lower shore. Barnacles made up a large fraction of the observations from Tatoosh Island (80%; Table 1); because of the very small sample size,

Table 1

Species composition of the diet of *Ocenebra lurida* and mean size of predator consuming each prey species from two sites. Observations for Turn Island were pooled over five days.

	Turn Island		Tatoosh Island	
Prey species	*n* (%)	Mean predator shell length (mm; ± SE)	*n* (%)	Mean predator shell length (mm; ± SE)
Limpets				
Tectura scutum	48 (20.8)	19.4 ± 0.55	—	
Lottia pelta	78 (33.8)	19.4 ± 0.38	2 (20)	19.3 ± 2.30
L. strigatella	1 (0.4)	21.1	—	
Total limpets	127 (55.0)		2 (20)	
Barnacles				
Semibalanus cariosus	71 (30.7)	19.3 ± 0.32	3 (30)	18.2 ± 1.86
Balanus glandula	17 (7.4)	19.1 ± 0.69	3 (30)	18.6 ± 1.89
B. nubilus	—	—	1 (10)	15.4
B. crenatus	3 (1.3)	19.5 ± 2.30	—	
Chthamalus dalli	6 (2.6)	17.9 ± 1.86	1 (10)	9.1
Total barnacles	97 (42.0)		8 (80)	
Other species				
Mytilus edulis	5 (2.2)	19.4 ± 0.42	—	
Calliostoma ligatum	1 (0.4)	18.9	—	
Spirorbis sp.	1 (0.4)	2.8	—	
Total other	7 (3.0)		—	
Total observations	231		10	

however, this value may not be representative for the population as a whole.

Predator-Prey Size Relations

For the two most commonly consumed species of limpets, *Tectura scutum* and *Lottia pelta,* both the mean size (log-transformed to homogenize the variance) and the size range of prey eaten increased with increasing predator size (Figures 2a, b). A similar trend was observed for the two most commonly consumed barnacle species, *Semibalanus cariosus* and *Balanus glandula,* but in both cases the increase in mean, log-transformed prey size was not significant (P = 0.096 and P = 0.24 respectively; Figure 2c). Somewhat surprisingly, a given sized *Ocenebra lurida* ate significantly larger *T. scutum* than *L. pelta* on average ($P < 0.001$, ANCOVA on log-transformed predator and prey shell lengths—a small, but statistically significant difference existed between the slopes [P = 0.033], but this would diminish rather than amplify the difference between adjusted means). For a mid-sized *O. lurida* (19.0 mm), the adjusted mean prey sizes were 18.6 mm (95% confidence interval = 16.0–21.5) and 9.7 mm (95% confidence interval = 8.7–10.9) respectively. In addition, over a broad range of predator size, the maximum size of *T. scutum* eaten exceeded that of *L. pelta* (Figures 2a, b).

Although the mean and range of sizes of prey eaten increased with increasing predator size, the average size of *Ocenebra lurida* eating a particular species of prey did not vary among prey species (Table 1; F = 0.272, P = 0.93; one-way ANOVA on predator shell length for all prey species for which more than five observations were recorded). One possible suggestion of a size-related dietary difference was the single observation of a 1.5-mm-diameter *Spirorbis* sp. being consumed by a 2.8-mm *O. lurida*; *Spirorbis* may serve as an alternative prey for very young snails.

Patterns of Drilling and Tissue Consumption in Limpets

When *Ocenebra lurida* attacked limpets, drill holes were clustered in the posterior half of the shell (82.8% and 86.4%), and nearly all (98.3% and 92.4% for *Tectura scutum* and *Lottia pelta* respectively) were within the perimeter of the pedal retractor muscle (Figure 3). All of these frequencies differ significantly from those expected if *O. lurida* drilled these regions in proportion to the area of the shell they represent (50% anterior vs. posterior, and 58.5% and 56.3% for the area internal to the muscle scar in *T. scutum* and *L. pelta* respectively; $P < 0.001$; with Yates' correction for continuity, χ^2 values all exceeded 23 for 1 df). A multiple-regression analysis revealed that larger *O. lurida* tended to drill closer to the apex than smaller ones, but this relationship was not strong (Figure 4) and was significant statistically only for *T. scutum* (Table 2). A similar analysis of drill-site location along the anteroposterior axis of limpets revealed no significant associations with predator or prey size. Hence, the site of attack did not depend strongly upon either predator or prey size.

Ocenebra lurida also appeared to consume limpet tissue

in a repeatable order (Table 3). Following completion of the drill hole, the gonad appeared to be eaten first, followed by the digestive gland, and both were completed before the foot was attacked. In only a small portion of the cases (8 of 58) was the foot actually being consumed. These were restricted to cases where the limpets were small relative to the size of the predator (Figure 5), although this pattern was not quite significant statistically ($P = 0.056$; contingency table analysis of counts of the ratio prey length : predator length that were pooled into four categories [<0.5, 0.5–0.99, 1.0–1.49, ≥1.5] to reduce the impact of small frequencies per cell).

Biases Associated with Feeding Observations During Low Tide

To assess whether feeding observations obtained at low tide were biased by differences in handling times (FAIRWEATHER & UNDERWOOD, 1983), at least with respect to the sizes of limpets being eaten by different sized *Ocenebra lurida*, attacks on limpets were divided into two groups based on whether drilling was still in progress or whether drilling was completed and flesh was being consumed. The proportion of completed drill holes declined with increasing limpet size for both species of limpets (Table 4a) but this decline was not significant statistically for either species or when both limpet species were analyzed simultaneously via a multi-way contingency table (Partial $P = 0.076$, Marginal $P = 0.075$ for dependence of hole status on limpet size; full analysis not presented—$P > 0.5$ for all remaining second and third order effects). In addition, although a higher overall proportion of drill holes had been completed on *Lottia pelta* than *Tectura scutum* (Table 4), this difference was also not significant ($\chi^2 = 0.36$, $P > 0.5$; 2 × 2 contingency table analysis). Curiously, when considering only those cases where drilling was still in progress, the degree of completion of the drill hole actually increased with increasing limpet size, although this relationship was significant statistically only for *L. pelta* ($P = 0.022$; Figure 6a).

The proportion of *Ocenebra lurida* that had completed drilling and were eating flesh did not vary dramatically with predator size either (Table 4b). The largest *O. lurida* were least likely to have completed drilling on both species of limpet; however, the overall trend with predator size was not consistent between species and the differences with predator size were only weakly significant for *Lottia pelta*. For the cases where drilling was still in progress, however, the degree of completion of the drill hole declined significantly with increasing predator size for *L. pelta* ($P = 0.007$; Figure 6b) but no such relationship was observed for *Tectura scutum* ($P = 0.9$; Figure 6b).

As a whole, when considering the larger of the two limpet species (*Tectura scutum*), the status of the drill hole in these observations made at low tide was unbiased with respect to either limpet or predator size. The only consistent bias these data revealed was a dependence of the proportion of drill hole completed on both limpet and predator size for the smaller sized limpet (*Lottia pelta*).

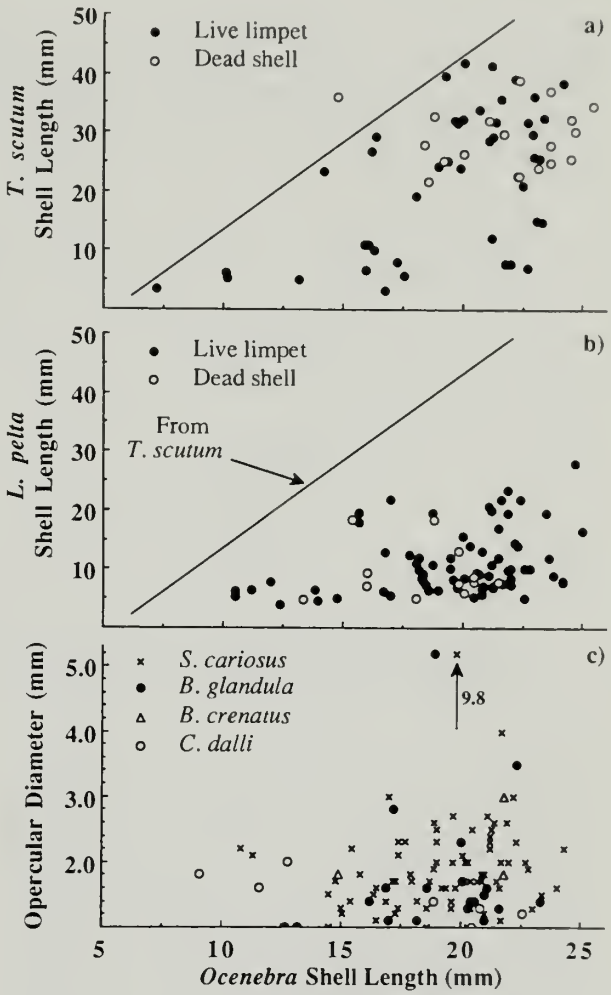

Figure 2

Prey size as a function of *Ocenebra lurida* shell length for six species of prey. (a) *Tectura scutum* (the line, fitted by eye, represents the upper limit to the size of limpet eaten where the predator size was known with certainty), (b) *Lottia pelta* (the line is identical to that in [a] for comparison), and (c) four species of barnacles. The regression equations of prey size (Y) on predator size (X) for the four most common prey species are (slope ± SE): *T. scutum*, $\log(Y) = 0.415 + 0.045 \pm 0.0080 \log(X)$ ($r^2 = 0.34$, $P < 0.001$, $n = 66$); *L. pelta*, $\log(Y) = 0.554 + 0.023 \pm 0.0064 \log(X)$ ($r^2 = 0.14$, $P < 0.001$, $n = 82$); *S. cariosus*, $\log(Y) = 0.059 + 0.011 \pm 0.0063 \log(X)$ ($r^2 = 0.04$, $P = 0.096$, $n = 74$); *B. glandula*, $\log(Y) = -0.147 + 0.018 \pm 0.0149 \log(X)$ ($r^2 = 0.077$, $P = 0.24$, $n = 20$).

Patterns of Drilling and Tissue Consumption in Barnacles

When attacking the barnacle *Semibalanus cariosus*, *Ocenebra lurida* drilled lateral plates almost exclusively and nearly half of these attacks occurred at the margins between

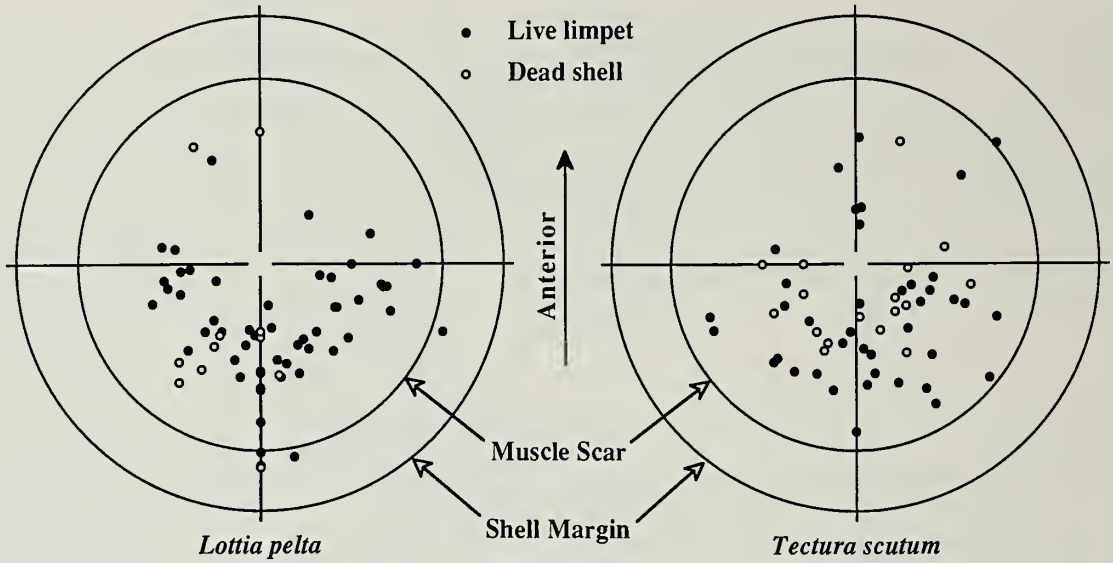

Figure 3

Polar coordinate plots of sites of attack by *Ocenebra lurida* on two species of limpets, *Lottia pelta* and *Tectura scutum*; distance from origin = (distance from apex to center of drill hole)/(distance from apex to shell margin in the same direction as the drill hole). Note that the origin of these figures corresponds to the apex of the shell even though the apices of these limpets are not precisely in the center of the shell.

plates (Table 5). Too few attack sites were noted for the remaining species to discern any patterns although, in contrast to *S. cariosus,* 3 of 5 attacks on *Balanus glandula* occurred at the opercular plates. For all barnacle species pooled, the frequency of attacks at the sutures between skeletal plates nearly equalled that through the plates.

Curiously, in the eight instances where the proboscis was observed unambiguously (six cases for *Semibalanus cariosus,* and one each for *Balanus glandula* and *Chthamalus*) it was always observed to be inserted between the opercular plates even though the site of drilling was located elsewhere. Similarly, in the 12 cases in which it was possible to verify that *S. cariosus* tissue had been consumed, the drill hole was found to be too small to permit passage of the proboscis: the diameter of final penetration was well less than half the outer diameter.

Maturity and Reproduction

On three dates, notes on the degree of closure of the siphonal canal and the sizes of copulating pairs were re-

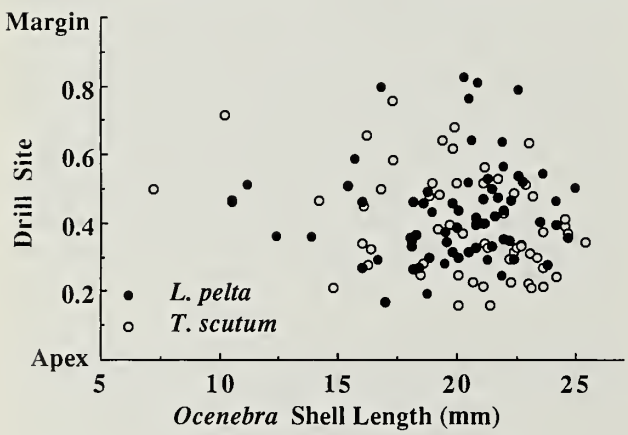

Figure 4

Location of drill site (expressed as proportion of distance from apex to margin of shell) as a function of *Ocenebra lurida* shell length for two species of limpets, *Lottia pelta* and *Tectura scutum* (see Table 2 for statistical analysis).

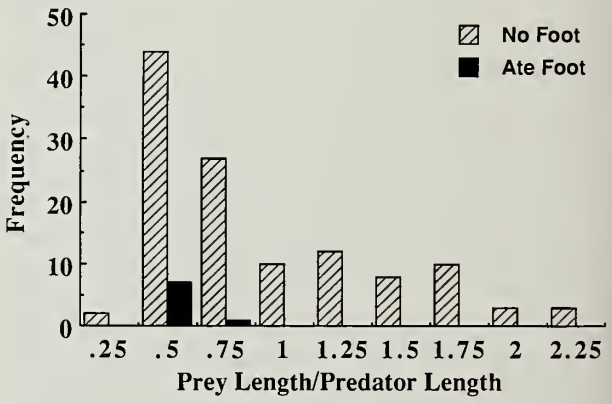

Figure 5

Frequency with which *Ocenebra lurida* was observed to be consuming the foot of limpets as a function of the ratio of the shell lengths of prey and predator. Data for *Tectura scutum* and *Lottia pelta* combined. No foot—other tissues had been consumed, but the foot was still intact. Ate foot—at least some portion of the foot had been consumed.

Table 2

Results from a multiple-regression analysis of drill hole position (dependent variable = proportion of distance from apex to shell margin) as a function of *Ocenebra lurida* and prey size (data in Figure 4).

	Lottia pelta	*Tectura scutum*
Coefficient		
Intercept	0.637	0.683
Ocenebra shell length (mm; ± SE)	−0.0081 ± 0.00547	−0.0150 ± 0.00604
Significance of coefficient (*P*)	0.15	0.016*
Limpet shell length (mm; ± SE)	−0.0042 ± 0.00355	0.0007 ± 0.00206
Significance of coefficient (*P*)	0.24	0.74
r^2	0.080	0.112
P (from ANOVA)	0.069	0.038*

* $P < 0.05$.

corded for *Ocenebra lurida* (Figure 7). Three categories of canal closure were recognized: fully open, transitional (beginning to close), and completely closed. Several lines of evidence suggest that the degree of closure of the siphonal canal reflects the state of maturity: (a) all individuals above 22 mm shell length had fully closed siphonal canals, (b) all individuals less than 16 mm had fully open siphonal canals, (c) snails noted actively copulating all had fully closed siphonal canals, and (d) the size distribution of copulating snails was indistinguishable statistically from that of solitary snails with closed canals ($\chi^2 = 2.06$, $P = 0.56$, for the four size categories: <18.9, 19.0–20.9, 21.0–22.9, ≥23). The siphonal canal thus does not appear to close intermittently over the life of an individual snail, a pattern which parallels rather closely that reported for *O. lumaria* (LUCKENS, 1970b). Using this criterion, maturity occurred around 16 to 19 mm shell length (Figure 7).

Although no egg capsules were noted, from 3 to 5 copulating pairs were observed (mean = 11% ± 3.2 SD, n = 4, range = 7.1–14.3% of all snails observed on each date) on all but the last date of observation at Turn Island (12 May). In addition, one copulating pair was observed out of 12 snails on Tatoosh Island on 5 July. Hence, although the reproductive season is by no means delimited by these data, they do indicate that active copulation was occurring in late spring and early summer and are consistent with the times of reproductive activity noted by SPIGHT *et al.* (1974).

Table 3

Frequencies with which *Ocenebra lurida* were observed to have consumed various portions of limpet flesh. Data from all limpet species pooled, but only for cases where the drill hole had been completed.

Tissues eaten	*n* (%)
None	8 (13.8)
Gonad only	30 (51.7)
Gonad + digestive gland only	12 (12.7)
Gonad + digestive gland + <50% of foot	3 (5.2)
Gonad + digestive gland + >50% of foot	5 (8.6)

DISCUSSION

Limpet-Feeding Habit

Ocenebra lurida appears to be an unusual member of the drilling gastropod fauna of the northeastern Pacific

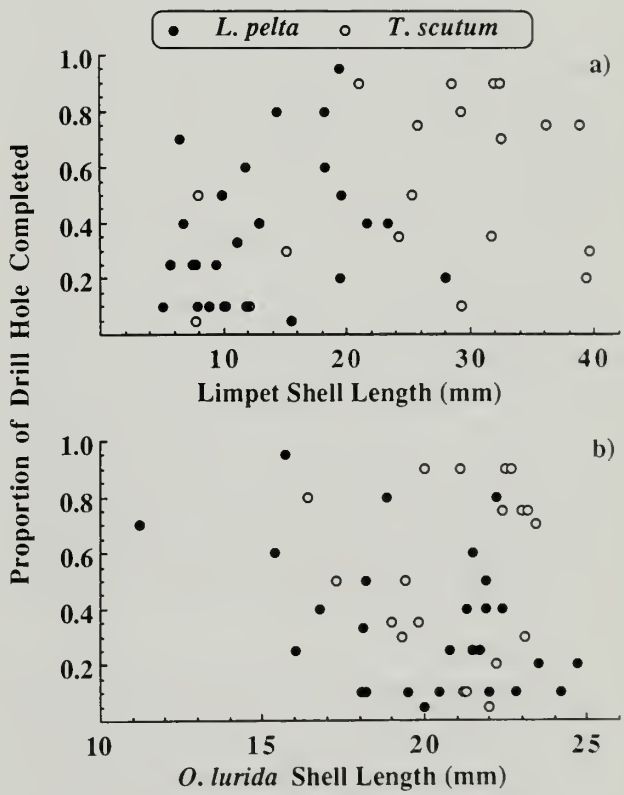

Figure 6

Proportion of drill hole completed through the shell as a function of limpet size (a) and size of *Ocenebra lurida* (b) for two species of limpets. Multiple regression equations for each limpet species are (coefficient ± SE): *Lottia pelta* (n = 27)—proportion completed = 0.018 ± 0.007(prey length, P = 0.022) − 0.042 ± 0.014(predator length, P = 0.007) + 0.959; *Tectura scutum* (n = 19)—proportion completed = 0.010 ± 0.007(prey length, P = 0.17) + 0.004 ± 0.035(predator length, P = 0.91) + 0.171.

Table 4

Frequencies at which *Ocenebra lurida* were found in the process of drilling vs. feeding on live limpets as a function of prey and predator size. Class limits are shell lengths (mm) and were chosen to obtain frequencies as nearly equal as possible. *P* values from two-way contingency table analyses.

a) Sizes of limpets in the process of being drilled or eaten

	Lottia pelta			*Tectura scutum*		
Prey percentile	Prey class limit	Drilled *n*	Eaten *n* (%)	Prey class limit	Drilled *n*	Eaten *n* (%)
Smallest ⅓	<7.8	5	16 (76.2)	<21.5	5	8 (61.5)
Middle ⅓		9	12 (57.1)		6	7 (53.8)
Largest ⅓	≥11.3	13	10 (43.5)	≥31.0	8	6 (42.9)
	$P = 0.088$			$P = 0.62$		

b) Sizes of *O. lurida* in the process of drilling or eating

	Lottia pelta			*Tectura scutum*		
Predator percentile	Predator class limit	Drilled *n*	Eaten *n* (%)	Predator class limit	Drilled *n*	Eaten *n* (%)
Smallest ⅓	<18.8	9	12 (57.1)	<19.4	4	9 (69.2)
Middle ⅓		5	17 (77.3)		6	7 (53.8)
Largest ⅓	≥21.3	13	9 (40.9)	≥22.0	9	5 (35.7)
	$P = 0.049$			$P = 0.22$		

because of the high frequency with which it consumes limpets (53.5%; Table 1). Limpets are at best rare in the diets of species of *Thais* (or *Nucella*) including *T. canaliculata* (1 out of 2001 observations), *T. emarginata* (4 of 2082 observations), *T. lamellosa* (0 of 889 observations), and *T. lima* (14 of 518 observations; all from PALMER, 1980). STIMSON (1970) also reported only a single instance of *T. emarginata* drilling a *Collisella scabra* and reported no attacks on *Lottia gigantea*. WEST (1986), on the other hand, reported that limpets (mainly *C. scabra*, but occasionally *Lottia limatula* [=*Collisella limatula*]) made up a somewhat

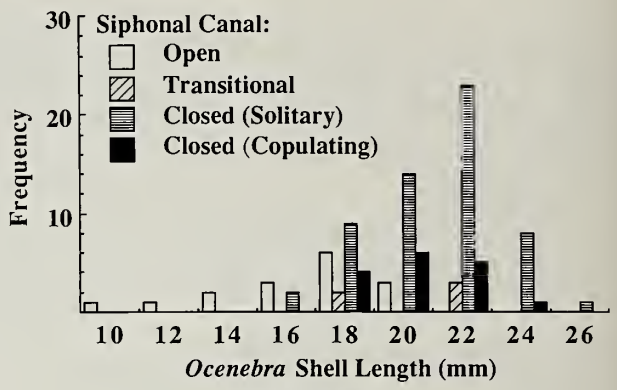

Figure 7

Frequency of *Ocenebra lurida* observed at different degrees of closure of the siphonal canal in the latter part of the study. Open—siphonal canal fully open, shell still exhibiting active recent growth; Transitional—siphonal canal beginning to close over, apertural lip beginning to thicken; Closed—fully closed siphonal canal, usually with a thickened lip, little or no evidence of recent shell growth (solitary—individual snails in the field; copulating—snails observed actively copulating in the field).

larger fraction of the diet overall for *T. emarginata* from central California (30 of 632 observations). Limpets are also uncommon in the diets of other thaidid gastropods from this geographic region. STIMSON (1970) noted that, when given a choice of *Mytilus edulis* and lottiid limpets in the lab, *Acanthina spirata* consumed mussels exclusively, and LUBCHENCO MENGE (1974) reported that *Acanthina punctulata* rarely consumed limpets (4 of 132 observations) even though limpets were available. Hence, at most, limpets make up less than 5% of the diet of thaidid gastropods from the northeastern Pacific.

Among non-drilling gastropods, *Searlesia dira* also consumes limpets regularly (from 10 to 31% of diet; LOUDA, 1979). However, because *Searlesia* appears to feed primarily via scavenging (LOUDA, 1979), the prevalence of limpets in the diet more likely reflects their availability as dislodged or moribund prey than a dietary preference.

Table 5

Frequencies of attack by *Ocenebra lurida* at various locations on the skeletal plates of barnacles; data from Turn Island and Tatoosh Island pooled.

	Opercular plates			Parietal plates			Unable to determine drill site
Prey species	At suture	Through	Total	At suture	Through	Total	
Semibalanus cariosus	—	1	1	17	20	37	13
Balanus glandula	3	—	3	1	1	2	5
B. crenatus	—	—	—	—	—	—	2
B. nubilus	—	—	—	1	—	1	—
Chthamalus dalli	—	—	—	1	—	1	2
Total (%)	3 (75.0)	1 (25.0)	4 (6.0)	20 (48.8)	21 (51.2)	41 (61.2)	22 (32.8)

The relative rarity of limpets in the diet of drilling gastropods from the northeastern Pacific is rather enigmatic for two reasons: (1) limpets are a common and conspicuous component of this rocky shore community and are consumed frequently by other predators which clearly recognize them as potential prey (MERCURIO *et al.*, 1985, and references therein), and (2) gastropods which prey frequently upon limpets are common on many other limpet-inhabited shores (BLACK, 1978; FAIRWEATHER *et al.*, 1984; MCQUAID, 1985; MENGE, 1973; MOORE, 1938; WEST, in press; reviewed in BRANCH, 1981), although not all of them attack limpets by drilling (*e.g.*, MENGE, 1973; MORAN, 1985). The rarity of limpets in the diet of thaidid gastropods from the northeastern Pacific is particularly curious for these reasons. Unfortunately the present data shed no light on this problem.

Perhaps limpets are a lower quality prey than the barnacles and mussels which make up the bulk of the diet of most thaidid gastropods (TAYLOR *et al.*, 1980). These alternative prey on which they grow rapidly (PALMER, 1983) may be sufficiently common and their availability may be sufficiently predictable that, when given a choice, thaidid gastropods simply reject limpets as undesirable on most occasions. Ironically, for the starfish *Leptasterias hexactis*, three of the four most energy rich prey in terms of calories per unit handling time were limpets, and limpets ranked highly both in terms of electivity in the field and in terms of laboratory choice experiments (MENGE, 1972). The low frequency of limpets in the diet of thaidid gastropods from the northeastern Pacific remains a puzzle.

Predator-Prey Size Relations

As in other predator-prey systems where the sizes of prey are comparable to that of the predator (BERRY, 1982; BROOM, 1982; HUGHES, 1980; LUBCHENCO MENGE, 1974; MENGE, 1972; PAINE, 1976; VERMEIJ, 1978), the average size of prey items eaten by *Ocenebra lurida*, as well as the size range, increased with increasing predator size. This pattern was most striking for the two most commonly consumed species of limpet (Figures 2a, b). A similar trend was observed for barnacles but it was not significant statistically, presumably because of the small size range of barnacles available at the site studied. The lack of feeding by small *O. lurida* on large limpets could reflect a physical constraint imposed by the maximum thickness of shell through which they can drill, as observed by KITCHELL *et al.* (1981) for *Polinices*. Alternatively, it could reflect a lower food value of large limpets to small *O. lurida*. In *Thais emarginata* such a decline occurs when small snails attack large mussels because, even though more tissue is available in larger prey, a small snail is unable to consume it rapidly enough before it begins to decompose (PALMER, 1980).

The observation that *Ocenebra lurida* ate larger *Tectura scutum* than *Lottia pelta* was unexpected. Unfortunately, because no measurements were taken on limpets accessible

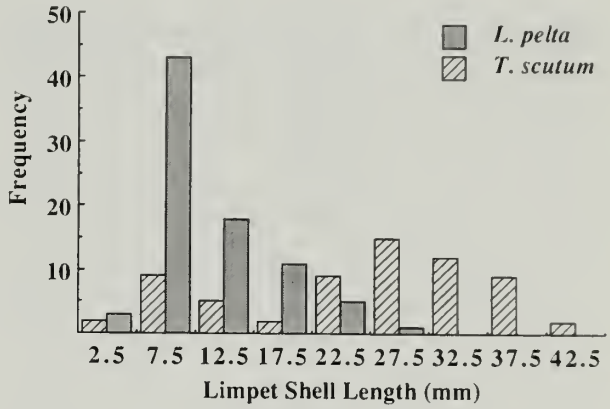

Figure 8

Size-frequency distribution of limpets (*Lottia pelta* and *Tectura scutum*) actually eaten by *Ocenebra lurida* at Turn Island over the duration of the study.

to but *not* eaten by *O. lurida*, some of this difference could have been due to differences in the average size of limpets occurring on the eastern shore of Turn Island. For example, although the average size of *T. scutum* eaten was greater than that of *L. pelta* (Figure 8), such differences could have resulted *either* from differences in the sizes available or differences in the sizes selected. *Tectura scutum* does reach a larger maximum adult size than *L. pelta* (MORRIS *et al.*, 1980), but average size of both species varies considerably among habitats. On nearby Turn Rock, the densities of these two species are quite similar (table 5 of DAYTON, 1971), but data on sizes were not presented. The lack of data on availability notwithstanding, however, larger limpets of both species *were* eaten by larger *O. lurida* (Figures 2a, b); hence, larger limpets were most likely also available to smaller *O. lurida* because they were intermingled on the shore.

Three hypotheses could account for the consumption of *Tectura scutum* to a larger size than *Lottia pelta*: (1) the two species may differ in the success of some escape behavior, (2) for limpets of the same shell length, the two species may differ in their food value, or (3) the two species may differ in their relative vulnerability to attack once captured. I am not aware of any data to address the first hypothesis for these prey species. *Lottia pelta*, however, do have a larger body mass for a given shell length than *T. scutum* (23% larger dry mass for a 20-mm limpet; 8.5 vs. 6.9 mg computed from MENGE [1972]). On this basis *L. pelta* should be *more* desirable as prey and hence eaten to a larger size assuming (1) that the handling times for limpets of the same shell length were comparable for both species, and (2) that energy per unit handling time decreases with increasing prey size, as it does above the "optimum" prey size (HUGHES, 1980).

Differences in shell thickness, however, seem more likely to account for the observed pattern of consumption. Over the size range of limpets where differences in maximum

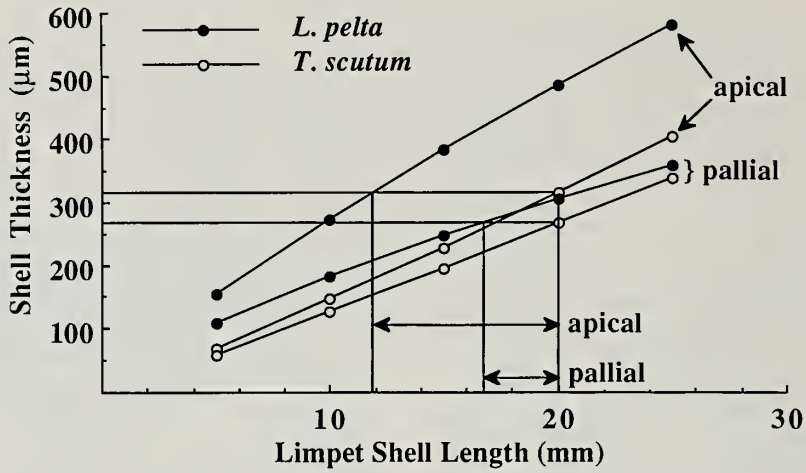

Figure 9

Comparison of shell thicknesses medial to the pedal retractor muscle for two species of limpets (computed from regressions of R. B. Lowell [unpublished data]). Apical—shell thickness at apex of shell; pallial—shell thickness just medial to the pedal retractor muscle. Horizontal and vertical lines illustrate how the expected difference in maximum size of vulnerability of *Lottia pelta* was estimated compared to a 20-mm *Tectura scutum*: if 20 mm was the maximum size of vulnerability of *T. scutum* to a given sized *Ocenebra lurida* (approximately 12.5 mm in this case; see Figure 2a) and if this maximum size of vulnerability was determined by the thickness of the limpet's shell, these lines indicate the shell length of *L. pelta* having the same medial shell thickness (12 mm based on apex thickness, 17 mm based on "pallial" thickness).

size eaten were detected (10–20 mm), *Lottia pelta* has a consistently thicker shell medial to the pedal retractor muscle than *Tectura scutum* (Figure 9). A thicker shell would lead to an increased handling time and hence it could result in a decreased food value for *L. pelta* if the longer handling time overwhelmed the benefits of the tissue mass differences noted above.

A thicker shell, on the other hand, may also reduce vulnerability by exceeding the depth to which a given sized *Ocenebra lurida* may drill. Assuming that the maximum size to which a limpet is vulnerable to a given sized *O. lurida* is determined by the depth to which it can drill (as observed for *Polinices* when drilling bivalves; KITCHELL *et al.*, 1981), then the expected *difference* in maximum size of vulnerability based on shell thickness may be calculated. This difference is on the order of 5 mm in shell length (the predicted value ranges from 3 mm based on shell thickness near the pedal retractor muscle, to 8 mm based on thickness at the apex comparing *Lottia pelta* to a *Tectura scutum* of 20 mm shell length; Figure 9). Rather remarkably, the *observed* difference in the maximum size of limpets eaten in this size range is approximately 7 mm shell length (Figure 2b). Furthermore, if this interpretation is correct, the maximum depth to which *O. lurida* can drill would be roughly 300 µm (Figure 9) for a 12.5-mm *O. lurida* (that size for which the maximum size of *T. scutum* eaten was approximately 20 mm; Figure 2a). In the absence of direct evidence for unsuccessful attacks, however, this estimate remains tentative.

Both *Lottia pelta* and *Tectura scutum* have similar shell microstructures (shell-structure group 1 of MACCLINTOCK, 1967); hence, microstructural differences would not account for differences in vulnerability between these species.

Two additional pieces of information suggest that the consumption of *Tectura scutum* to a larger size than *Lottia pelta* may have an energetic rather than a mechanical basis. First, FRANK (1982) reports that black oystercatchers (*Haematopus bachmani*) consume *L. pelta* to a smaller size than *T. scutum* (approximately 10 vs. 14 mm shell length). Second, data of G. M. Branch (unpublished observations), also on feeding by *H. bachmani*, yield selectivity curves whose peaks and whose upper and lower limits are consistently on the order of 5 to 10 mm shell length larger for *T. scutum* than *L. pelta*. These data, taken from five separate areas of shore, indicate that *H. bachmani* also prefers larger *T. scutum* than *L. pelta*. The remarkably similar patterns of size preference exhibited by both *H. bachmani* and *Ocenebra lurida* seem unlikely to be due to mechanical properties of the shell or foot given the radically different modes of attack of these two predators. Rather, these size preferences would seem most simply accounted for by differences in the flesh weight-shell length ratios between these two species of limpet.

Attack Behavior

Compared to other limpet and barnacle predators, *Ocenebra lurida* used very similar modes of attack. In particular, when attacking limpets, its behavior is strikingly similar to that of *Dicathais aegrota* of Western Australian shores (BLACK, 1978). Both species attack preferentially the posterior region of the limpet shell within the perimeter of the pedal retractor muscle (Figure 3). As suggested by

Black, the presumed adaptive value of such a behavior lies in the more immediate access to the energy-rich gonad and digestive gland. Because snails which drill limpets run the risk of being dislodged when the limpet releases hold of the substratum, and also because they may be unable to consume all the tissue before losing hold of their once-moribund prey, they would benefit from consuming these energy-rich tissues first.

That the gonad and digestive gland were consumed prior to the foot (Table 3) is due in part to their anatomical relation to the site of attack, but the actual order of tissue consumption was not quite so simplistic. If tissue were consumed purely as a function of proximity to the drill hole, portions of the foot would be consumed before the gonad and digestive gland had been completed because the distance from the shell to the foot is less than from the posterior to the anterior end of the viscera. Yet I commonly observed viscera being consumed to a greater distance anterior to the drill hole than the distance from the drill hole to the foot.

The observation that limpet feet were consumed exclusively in cases where the limpet was smaller than the predator (Figure 5) suggests that *Ocenebra lurida* may, in fact, not be able to retain its hold upon larger limpets to permit all the flesh to be consumed. This would provide another advantage to the preferential consumption of viscera. These observations do not appear to be biased by differences in handling times because drill holes were not significantly more likely to have been completed on small limpets compared to larger ones (Table 4; for an extensive discussion of such biases see FAIRWEATHER & UNDERWOOD, 1983).

When attacking barnacles, *Ocenebra lurida* exhibited a number of behaviors in common with thaidid gastropods (HART & PALMER, 1987; PALMER, 1982). First, drilling occurred preferentially at the margins of plates rather than through them (Table 5): nearly half of all attacks at lateral plates (20 of 41) occurred at regions of plate overlap even though such regions make up only about 15% of the periphery of the barnacle's skeletal wall (PALMER, 1982). Second, even where tissue had been consumed, most of the drill holes were not enlarged enough to permit passage of the proboscis. Coupled with the few observations where *O. lurida* consumed barnacles from between the gaping opercular plates even though they had been drilled elsewhere, these observations suggest rather strongly that *O. lurida* produces a narcotizing toxin which relaxes barnacles. In this manner, the flesh may be consumed without the additional time and effort required to enlarge the drill hole.

Biases in Feeding Observations Obtained at Low Tide

Although differences in handling times for different prey types may create biases in the "apparent" diet of intertidal predators observed feeding at low tide (FAIRWEATHER & UNDERWOOD, 1983), the data obtained for *Ocenebra lurida* attacking limpets suggest that such biases had little if any effect on the observed diet. Although drill holes were more likely to have been completed on smaller limpets, this trend was not significant statistically for either limpet species (Table 4). In addition, unfinished drill holes were closer to completion in larger compared to smaller limpets (Figure 6a), a pattern not consistent with the bias expected based on shorter handling times for small limpets.

Rather than revealing a size bias in handling times, the proportion of drill hole completed (Figure 6) seems more likely to reflect the time since an attack was initiated. Because feeding *Ocenebra lurida* were interrupted at random with respect to both predator and prey size, the observations for *Lottia pelta* suggest that *O. lurida* had been drilling larger limpets for a longer time prior to tidal emersion than smaller ones (Figure 6a) and that, following tidal immersion, larger *O. lurida* initiated attacks on limpets earlier than smaller ones (Figure 6b). Multiple-regression analysis revealed that both of these relationships were significant (Figure 6 legend).

Comparison of Diets with Other Species of *Ocenebra*

The paucity of published data precludes very strong conclusions, but the extensive consumption of limpets by *Ocenebra lurida* does appear to differ from the diets of other species of *Ocenebra*. Because of their status as pests, two species are known to prey on commercially grown oysters: the European *O. erinacea* (BARRY, 1981; HANCOCK, 1960; ORTON, 1929), and the western Pacific (but now widely distributed in the NE Pacific via incidental introductions; CARLTON, 1979) *O. japonica* (CHEW & EISLER, 1958; CHAPMAN & BANNER, 1949; considered to be *Ceratostoma inornatum* by RADWIN & D'ATTILIO [1976]). *Ocenebra erinacea* also consumes other prey including both burrowing (*Tapes, Cardium, Mercenaria, Paphia*; HANCOCK, 1960; PIÉRON, 1933) and epifaunal (*Pecten*; PIÉRON, 1933) bivalves, "barnacles, small tubicolous worms, mussels and anomiid bivalves" and possibly *Crepidula* (FRETTER & GRAHAM, 1962:516). For *O. japonica* (=*Ceratostoma inornatum*) oysters appear to be a less desirable prey because, when given a choice, both *Mytilus edulis* and *Tapes japonica* (=*Venerupis japonica*) were eaten more frequently (42.6% and 36.5% respectively) than oysters (20.9%) when all were of comparable size (CHEW & EISLER, 1958). This contrasts with the conclusions of CHAPMAN & BANNER (1949) who reported that oysters were eaten in preference to barnacles and mussels in the laboratory, but their experiments were much less well designed to detect preferences. In Netarts Bay, Oregon, the bivalves *Macoma balthica* and *Clinocardium nuttalli* form the bulk of the diet of *O. japonica* (SQUIRE, 1972 [cited in CARLTON, 1979:384]).

Individuals of the Japanese *Ocenebra lumaria* (also considered to be *Ceratostoma inornatum* by RADWIN & D'ATTILIO [1976]) are reported to eat several species of barnacles (*Chthamalus challengeri, Balanus trigonus, B. albicostatus*, and *B. tintinabulum*) and mussels (*Mytilus edulis*

and *Septifer virgatus*) when these are made available in the laboratory, and when given a choice they prefer *Chthamalus* over *Mytilus* (LUCKENS, 1970a). Except for noting that hatchlings were observed to consume newly settled *Chthamalus*, however, no field observations of diet were reported. Similarly, although providing extensive data on growth and survival, FOTHERINGHAM (1971) mentions only incidentally the diet of the eastern Pacific *O. poulsoni*; they appear to consume boring bivalves primarily (*Penitella penita* and *Lithophaga plumula*; p. 743) at least as adults, while young snails "occasionally feed on barnacles" (p. 750). Similarly, although providing data on growth rates and natural densities for both *O. interfossa* and *O. lurida*, only laboratory observations of feeding by *O. lurida* on *Balanus glandula* and *M. edulis* were reported by SPIGHT *et al.* (1974) who noted that barnacles were eaten in preference to mussels. Finally, TALMADGE (1975) merely reports some anecdotal observations of *O. lurida* rasping pits in the girdle of *Cryptochiton stelleri*, but makes no mention of any other feeding observations, and KILBURN & RIPPEY (1982) report anecdotal observations for the South African *O. purpuroides* which appears to feed on "small tube worms."

As in any local field study, I cannot be sure how representative the diet I have reported is for *Ocenebra lurida* as a whole. I initiated this study specifically because of the rather high densities of *O. lurida* at this intertidal site (approx. 1–3/m^2) and barnacles and mussels happened to be relatively uncommon here. Although I have since observed comparable densities in a relatively wave-exposed cobble and boulder habitat on Cape Beale (Vancouver Island), I have normally encountered *O. lurida* only as scattered individuals at a density well less than 1/m^2 on intertidal shores. Subtidally, however, they may achieve higher densities: SPIGHT *et al.* (1974) report a density of 4.25/m^2 on a subtidal rock wall.

These unfortunately meagre data, diminished further if indeed both *Ocenebra japonica* and *O. lumaria* are correctly *Ceratostoma inornatum* (RADWIN & D'ATTILIO, 1976), permit little to be said here except that, like many muricacean genera (TAYLOR *et al.*, 1980) diets appear to vary considerably among the different species of *Ocenebra*. Whether the diet of *O. lurida* is really unusual for the genus awaits further field studies.

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LITERATURE CITED

BARRY, M. D. 1981. Distribution and ecology of oysters, *Ostrea edulis* (L.), in Kilkieran and Bertraghboy bays, Connemara, Co. Galway. Irish Fish. Invest. (Ser. B) 24:1–18.

BERRY, A. J. 1982. Predation by *Natica maculosa* Lamarck (Naticidae: Gastropoda) upon the trochacean gastropod *Umbonium vestiarium* (L.) on a Malaysian shore. Jour. Exp. Mar. Biol. Ecol. 64:71–89.

BLACK, R. 1978. Tactics of whelks preying on limpets. Mar. Biol. 46:157–162.

BRANCH, G. M. 1981. The biology of limpets: physical factors, energy flow, and ecological interactions. Oceanogr. Mar. Biol. Ann. Rev. 19:235–380.

BROOM, M. J. 1982. Size-selection, consumption rates and growth of the gastropods *Natica maculosa* (Lamarck) and *Thais carinifera* (Lamarck) preying on the bivalve *Anadara granosa* (L.). Jour. Exp. Mar. Biol. Ecol. 56:213–233.

CARLTON, J. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Ph.D. Dissertation, University of California, Davis. 904 pp.

CHAPMAN, W. M. & A. H. BANNER. 1949. Contributions to the life history of the Japanese drill, *Tritonalia japonica*, with note on other enemies of the Olympia oyster, *Ostrea lurida*. State of Washington, Dept. Fish. Biol. Bull. 49A:169–200.

CHEW, K. K. & R. EISLER. 1958. A preliminary study of the feeding habits of the Japanese oyster drill, *Ocinebra japonica*. Jour. Fish. Res. Bd. Canada 15:529–535.

DAYTON, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351–389.

DIXON, W. J. 1983. BMDP statistical software. University of California Press: Berkeley.

FAIRWEATHER, P. G. & A. J. UNDERWOOD. 1983. The apparent diet of predators and biases due to different handling times of their prey. Oecologia 56:169–179.

FAIRWEATHER, P. G., A. J. UNDERWOOD & M. J. MORAN. 1984. Preliminary investigations of predation by the whelk *Morula marginalba*. Mar. Ecol. Progr. Ser. 17:143–156.

FOTHERINGHAM, N. 1971. Life history patterns of the littoral gastropods *Shaskyus festivus* (Hinds) and *Ocenebra poulsoni* Carpenter (Prosobranchia: Muricidae). Ecology 52:742–757.

FRANK, P. W. 1982. Effects of winter feeding on limpets by black oystercatchers, *Haematopus bachmani*. Ecology 63:1352–1362.

FRETTER, V. & A. GRAHAM. 1962. British prosobranch molluscs. Ray Society: London. 755 pp.

HANCOCK, D. A. 1960. The ecology of the molluscan enemies of the edible mollusc. Proc. Malacol. Soc. Lond. 34:123–143.

HART, M. W. & A. R. PALMER. 1987. Stereotypy, ontogeny, and heritability of drill site selection in thaidid gastropods. Jour. Exp. Mar. Biol. Ecol. 107:101–120.

HUGHES, R. N. 1980. Optimal foraging in the marine context. Oceanogr. Mar. Biol. Ann. Rev. 18:423–481.

KILBURN, R. & E. RIPPEY. 1982. Sea shells of southern Africa. Macmillan South Africa Ltd.: Johannesburg. 249 pp.

KITCHELL, J. A., C. H. BOGGS, J. F. KITCHELL & J. A. RICE. 1981. Prey selection by naticid gastropods: experimental tests and application to the fossil record. Paleobiology 7:533–552.

KOZLOFF, E. N. 1987. Marine invertebrates of the Pacific Northwest. Univ. Washington Press: Seattle, Washington. 511 pp.

LINDBERG, D. R. 1986. Name changes in the "Acmaeidae." Veliger 29:142–148.

LOUDA, S. M. 1979. Distribution movement and diet of the snail *Searlesia dira* in the intertidal community of San Juan Island, Puget Sound, Washington. Mar. Biol. 51:119–131.

LUBCHENCO MENGE, J. 1974. Prey selection and foraging period of the predaceous rocky intertidal snail, *Acanthina punctulata*. Oecologia 17:293–316.

LUCKENS, P. A. 1970a. Predation and intertidal zonation at Asamushi. Bull. Mar. Biol. Stn. Asamushi 14:33–52.

LUCKENS, P. A. 1970b. Variation of shell characters of a species of *Ocenebra* (Mollusca: Gastropoda) at Asamushi. Sci. Rep. Tohoku Univ. Ser. IV (Biol.) 35:149–159.

MACCLINTOCK, C. 1967. Shell structure of patelloid and bellerophontoid gastropods (Mollusca). Peabody Mus. Natur. Hist., Yale Univ., Bull. 22:1–140.

MCQUAID, C. D. 1985. Differential effects of predation by the intertidal whelk *Nucella dubia* (Kr.) on *Littorina africana knysnaensis* (Phillipi) and the barnacle *Tetraclita serrata* Darwin. Jour. Exp. Mar. Biol. Ecol. 89:97–107.

MENGE, B. A. 1972. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. Ecol. Monogr. 42:25–50.

MENGE, B. A. 1973. Effect of predation and environmental patchiness on the body size of a tropical pulmonate limpet. Veliger 16:87–92.

MERCURIO, K. S., A. R. PALMER & R. B. LOWELL. 1985. Predator-mediated microhabitat partitioning by two species of visually cryptic, intertidal limpets. Ecology 66:1417–1425.

MOORE, H. B. 1938. The biology of *Purpura lapillus*. Part III. Life history and relation to environmental factors. Jour. Mar. Biol. Assoc. U.K. 23:67–74.

MORAN, M. J. 1985. Effects of prey density, prey size and predator size on rates of feeding by an intertidal predatory gastropod *Morula marginalba* Blainville (Muricidae), on several species of prey. Jour. Exp. Mar. Biol. Ecol. 90:97–105.

MORRIS, R. H., D. P. ABBOTT & E. C. HADERLIE. 1980. Intertidal invertebrates of California. Stanford Univ. Press: Stanford. 690 pp.

ORTON, J. H. 1929. Habitats and feeding habits of *Ocinebra erinacea*. Nature 124:370–371.

PAINE, R. T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. Ecology 57:858–873.

PALMER, A. R. 1980. A comparative and experimental study of feeding and growth in thaidid gastropods. Ph.D. Dissertation, University of Washington, Seattle. 320 pp.

PALMER, A. R. 1982. Predation and parallel evolution: recurrent parietal plate reduction in balanomorph barnacles. Paleobiology 8:31–44.

PALMER, A. R. 1983. Growth rate as a measure of food value in thaidid gastropods: assumptions and implications for prey morphology and distribution. Jour. Exp. Mar. Biol. Ecol. 73:95–124.

PIÉRON, H. 1933. Notes éthologiques sur les gastéropodes perceurs et leur comportment avec utilisation de méthodes statistiques. Arch. Zool. Exp. Gén. 75:1–20.

RADWIN, G. E. & A. D'ATTILIO. 1976. *Murex* shells of the world. Stanford Univ. Press: Stanford, California. 284 pp.

SPIGHT, T. M., C. BIRKLAND & A. LYONS. 1974. Life histories of large and small murexes (Prosobranchia: Muricidae). Mar. Biol. 24:229–242.

SQUIRE, D. R. 1972. The Japanese oyster drill, *Ocenebra japonica*, in Netarts Bay, Oregon. M.S. Thesis, Oregon State University. 65 pp.

STIMSON, J. 1970. Territorial behavior of the owl limpet, *Lottia gigantea*. Ecology 51:113–118.

TALMADGE, R. R. 1975. A note on *Ocenebra lunda*. Veliger 17: 414.

TAYLOR, J. D., N. J. MORRIS & C. N. TAYLOR. 1980. Food specialization and the evolution of predatory prosobranch gastropods. Paleontology 23:375–409.

VERMEIJ, G. J. 1978. Biogeography and adaptation. Patterns of marine life. Harvard Univ. Press: Cambridge, Massachusetts. 332 pp.

WEST, L. 1986. Interindividual variation in prey selection by the snail *Nucella* (=*Thais*) *emarginata*. Ecology 67:798–809.

WEST, L. In press. Prey selection by the tropical snail *Thais melones*: a study of interindividual variation. Ecology.

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Growth of Three Species of Abalones (*Haliotis*) in Southern California

by

THEODORE C. TUTSCHULTE AND JOSEPH H. CONNELL[1]

Department of Biological Sciences, University of California,
Santa Barbara, California 93106, U.S.A.

Abstract. Growth of tagged juvenile pink abalones (*Haliotis corrugata*) in the field and laboratory ranged from 11 to 16 mm per yr; adult annual growth ranged from 4 to 8 mm. Adults transplanted from shallow water to near their lower depth limit grew hardly at all. Juvenile green abalones (*H. fulgens*) tagged in the field and laboratory grew from 13 to 16 mm per yr; adult annual growth ranged from 4 to 7 mm. Transplants to depths below the normal limit did not grow. For white abalones (*H. sorenseni*) in the laboratory, juveniles grew 25 mm per yr, adults grew 10 mm per yr. In the field adults showed little shell growth, probably because they actively eroded their shells on the experimental tiles to which they had been transplanted. In all species smaller individuals grew faster in absolute length than did larger ones, independent of treatment. Growth rates calculated from polymodal size frequency analyses agreed closely with those from direct observations of tagged individuals. Based on these data, von Bertalanffy growth curves were constructed. Relative growth in soft-body weight decreased gradually with increasing size. All three species showed seasonal variations in growth; each species had a different season of maximum growth. During the autumn when gonad growth occurs in adult pink abalones, growth was significantly lower than in the preceding summer or the following winter. Juvenile pink abalones did not show this pattern. These results suggest that there may be a shift in energy allocation into reproduction and away from growth in this species. Adult pinks and greens would eventually reach a maximum size in about 50 yr; whites would do so in about 34 yr.

INTRODUCTION

This study was undertaken as part of a comparative investigation of three species of abalones, *Haliotis fulgens* Philippi, *H. corrugata* Wood, and *H. sorenseni* Bartsch, referred to here as the green, pink, and white abalones respectively, in southern California. Growth rates are important indicators of well-being in a population and are also useful in estimating age when no other direct method, such as annual rings, is available. We have measured variations in growth rates under different environmental conditions and in different seasons for the three species and have compared these to the growth of other species elsewhere. We have also fitted mathematical models of growth with age to make predictions for older ages where data are scarce.

AREA AND METHODS

All collections were made between April 1969 and April 1973 in the Isthmus region of Santa Catalina Island within an 800-m radius of the coordinates 33°27′N, 118°29′W. The depths and frequency of collections are described in more detail below. This area faces the mainland across the 32-km-wide San Pedro Channel and thus is protected from westerly and southwesterly oceanic swells and the occasional southeasterly storms occurring in this region, but is exposed to wind and waves from the northwest, north, and northeast. Except for periods of northwest storms, there is very little wave action, but the area is regularly swept by strong tidal currents that sometimes reach a speed of 3 knots. There are dense beds of giant kelp (*Macrocystis pyrifera* (Linnaeus) C. A. Agardh) along the shore and on offshore reefs. These beds extend from approximately 2 to 20 m below MLLW. A dense understory beneath the *Macrocystis* canopy is comprised of a variety of red and brown algae. Between the 20- and 40-m-depth levels, the large leaf kelps *Laminaria farlowii* Setchell and *Agarum fimbriatum* Harvey are the dominant algal forms.

Direct Observations of Marked Individuals

We followed the growth of individual abalones (1) under laboratory conditions, (2) in cages on the sea floor, and

[1] Reprint requests should be sent to the second author.

(3) marked, released in the wild, and then recaptured. For these studies, each animal was marked with a numbered stainless steel tag attached to the shell by means of a stainless steel wire looped through two adjacent respiratory pores, similar to CROFTS (1929). A notch was filed in the shell margin in such a way that a small triangular area of nacre would remain exposed on the outer shell surface following shell growth (LEIGHTON, 1968), thus assuring that growth could still be measured in the event of loss of the tag. Growth was measured as the increment to anterior-posterior shell length. Weight-length relationships were determined for each species from large series of animals collected and killed for reproductive studies (TUTSCHULTE & CONNELL, 1981).

In the laboratory, animals were held in running, aerated, ambient seawater at the University of California, Santa Barbara, with food (blades of *Macrocystis pyrifera*) always present. Each animal was remeasured at intervals for one or more years. In the field, three different types of experiments were done. In the first, animals held in cages on the sea floor were provided with refuges consisting of 30 × 15 × 2.5-cm clay roofing tiles stacked with 2.5-cm spacers between them. Each rack of tiles was enclosed in a cage constructed of neoprene mesh having square openings 8 mm on a side. Food, consisting of the various brown and red algae in approximately the same proportions as encountered by the abalones in nature (TUTSCHULTE & CONNELL, in press), was put into each cage at monthly intervals and in sufficient quantity that some algae remained at the end of each interval between feedings. The cages were placed at depths of 2 and 9 m. The animals were remeasured at 3- to 4-month intervals over periods of up to 13 months. In this series, new animals suitably tagged were added between intervals to replace abalones that had died. The second field series consisted of releasing marked pink and green abalones at 5 m depth on natural substrates from which all abalones had been removed; survivors were remeasured after 1 yr. In the third field series, abalones whose shell margins had been notched, but which were not individually tagged, were released onto a pile of roofing tiles at 9 and at 20 m. The tiles had been arranged on the sea floor several months before the abalones were released onto them and thus had been leached and had accumulated a growth of benthic diatoms and attached algae, which provided food for the smaller abalones.

Growth Estimates from Analyses of Size-Frequency Data

A method of estimating growth from an analysis of polymodal size-frequency distributions using probability paper (HARDING, 1949; CASSIE, 1950, 1954) was used to extract year classes from population samples taken at intervals over a 2-yr period. This method dissects the observed polymodal curves into a series of overlapping normal curves. Information on spawning times (TUTSCHULTE & CONNELL, 1981) was used to estimate the age of each mode. For example, since the greens have a single spawning season in July–August each year, the age of each mode of a sample taken in April was estimated to be a year class plus 0.75 yr. Thus, the zero-year class in that sample was estimated to be 9 months old, the one-year class to be 21 months old, and so on. Calculated growth rates for comparison to those directly observed were derived from a linear regression of mean shell lengths of year classes on estimated ages for the first 4 yr for pinks and first 6 yr for greens and whites.

The use of length-frequency analysis allows us to link growth to age, using the fitted growth curves described below. However, it is necessarily a less direct method for estimating growth than observations of marked individuals. Therefore, we used it only after comparing its results to those from the direct observations. The two methods gave very similar results (Table 1).

While many workers have applied the probability paper method used here (HARDING, 1949; CASSIE, 1950, 1954; NEWMAN, 1968; POORE, 1972; TUTSCHULTE, 1976; SAINSBURY, 1982), other statistical methods have also been developed to separate year classes in length-frequency data (*e.g.*, HASSELBLAD, 1966; YONG & SKILLMAN, 1975; MCNEW & SUMMERFELT, 1978; MACDONALD & PITCHER, 1979; SCHNUTE & FOURNIER, 1980; FOURNIER & BREEN, 1983; SHEPHERD & HEARN, 1983). In one instance (SAINSBURY, 1982) the probability paper method of CASSIE (1950) was compared to the statistical method of YONG & SKILLMAN (1975), using data from an abalone in New Zealand. In 13 of 15 comparisons of the mean length of a particular age class, the estimates of the two methods differed by less than 8%. Thus, the two methods gave quite similar estimates of size at a given age for an abalone. The closeness of this comparison, and the similarity of the growth rates from our direct observations to those calculated by the probability paper method, lend confidence to this method.

Fitted Growth Curves

To describe the growth of abalones mathematically, we used growth models developed for fish populations (RICKER, 1975). Early work by BRODY (1927) described the increase in length of domestic animals as an S-shaped growth curve, with the early growth stanzas having an increasing slope over time and the later ones having a decreasing slope. Since our growth measurements were mainly on animals older than about 0.3 yr, we have assumed, as in most work on growth of fish and invertebrates, that this growth is best described by a curve of decreasing slope.

We have used two different growth models. The first was proposed by VON BERTALANFFY (1934, 1938, 1960). FABENS (1965) has derived the following simplified equation for the von Bertalanffy growth curve for length vs. age:

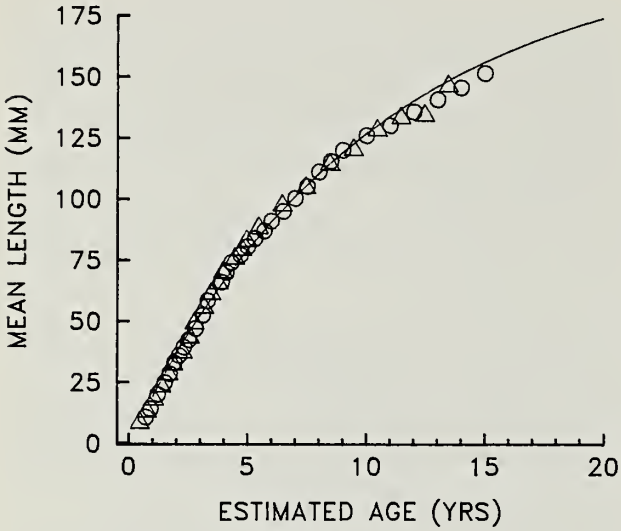

Figure 1

Growth of pink abalones (*Haliotis corrugata*). The points shown as O and △ were derived from analyses of polymodal size frequencies from pooled samples taken in 1971 and 1972, $n = 509$ and 685, respectively. The continuous curve was calculated from a von Bertalanffy equation, with $K = 0.097$ and asymptotic size of 202 mm (see text).

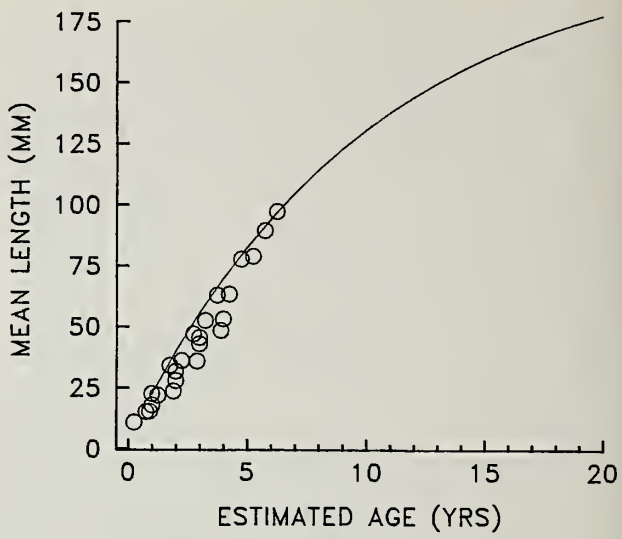

Figure 2

Growth of green abalones (*Haliotis fulgens*). The points were determined from analyses of polymodal size frequencies from pooled samples taken in 1970 to 1972, $n = 444$. The continuous curve was calculated from a von Bertalanffy equation, with $K = 0.101$ and asymptotic size of 205 mm (see text).

$$L = L_\infty(1 - be^{-Kt}). \quad (1)$$

This is a curve of the decaying exponential type in which the animal reaches half of the difference between length at birth (equivalent to the size at which they settle on the substrate from the plankton), L_0, and the asymptotic maximum length, L_∞, at age $t = \ln 2/K$. Because the von Bertalanffy growth equation fits the growth data of a wide variety of animals (*e.g.*, fish, mammals, and many invertebrates, including some prosobranch mollusks) and because "... the underlying concepts are ... the most satisfactory of those which have so far been put forward ..." (BEVERTON & HOLT, 1957), the model has gained rather wide acceptance among biologists, at least for descriptive purposes, and has been incorporated into methods devised for estimating individual growth rates and population mortality rates from size data for fish or various invertebrates (*e.g.*, BEVERTON, 1954; FABENS, 1965; GREEN, 1970; EBERT, 1973, 1975, 1980; SCHNUTE & FOURNIER, 1980), including abalones (*e.g.*, FORSTER, 1967; NEWMAN, 1968; POORE, 1972; TUTSCHULTE, 1976; HAYASHI, 1980; SAINSBURY, 1982; SHEPHERD & HEARN, 1983; FOURNIER & BREEN, 1983).

The von Bertalanffy curves for each species in Figures 1-3 were obtained by setting L_∞ of equation (1) equal to the maximum size that we have observed for each species and L_0 equal to 1.0 mm at age 0.1 yr (LEIGHTON, 1972, found that white abalones reached 0.7 mm at 0.1 yr in the laboratory). The value for t at length $(L_\infty + L_0)/2$ was determined from the data in Figures 1-3, which were obtained from size-frequency data as described above (see TUTSCHULTE, 1976, for details). This t value was then used in the model relationship $t = \ln 2/K$ at length $(L_\infty + L_0)/2$ to calculate K (FABENS, 1965). The third parameter b becomes eliminated by algebraic manipulation as shown by FABENS (1965).

A second mathematical equation of the decaying exponential type was used to calculate growth coefficients and asymptotic sizes from data on direct observations of marked individuals. FORD (1933) (see also WALFORD, 1946) developed the expression:

$$L_{t+1} = L_\infty(1 - k) + kL_t \quad (2)$$

where the growth coefficient $k = e^{-K}$, in which K is the von Bertalanffy coefficient in equation (1). This equation expresses a type of growth in which the increment in each year is less than that in the previous year by the fraction $(1 - k)$ of the latter (RICKER, 1975). If L_{t+1} is regressed against L_t, k is the slope of the line and the intercept is L_∞ $(1 - k)$, from which L_∞ can be calculated. These regressions were calculated from direct measurements of marked individuals, with L_t being the initial length and L_{t+1} being the length after 1 yr.

The von Bertalanffy equation (1) can be used to predict the age at any future size. From it FABENS (1965) derived the following equation (his equation 4.1):

$$L_{t+\Delta t} = L_t + (L_\infty - L_t)(1 - e^{-K\Delta t}). \quad (3)$$

Rearranging and solving for Δt:

$$\Delta t = \ln[1 - (L_{t+\Delta t} - L_t)/(L_\infty - L_t)]/-K. \quad (4)$$

We used equation (4) to calculate the average age at which

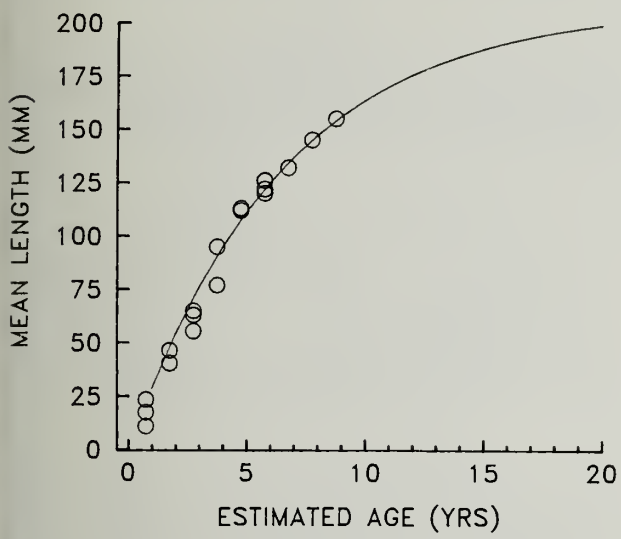

Figure 3

Growth of white abalones (*Haliotis sorenseni*). The points indicate the individual values from Table 4. The continuous curve was calculated from a von Bertalanffy equation, with $K = 0.154$ and asymptotic size of 210 mm (see text).

an abalone would grow to within 1 mm of its asymptotic size.

RESULTS

Annual Growth of Marked Individuals

Laboratory growth: Increments of shell lengths of pink, green, and white abalones held in the laboratory are given in Table 1. These growth rates show the same pattern evident in the rates obtained by the other three methods: small whites grow about twice as fast as small pinks and greens, the latter two species appearing to grow at quite similar rates.

Growth in the field: The average growth rate of the group of pinks <100 mm initial length released on tiles at 9 m depth was about ⅓ higher than that of those held in cages nearby at the same depth (Table 1). Of a large group of tagged juvenile pinks released at 5 m depth in a 20-m² area of natural substrate from which all abalones had been previously removed, 16 survivors were recovered over a year later. This group grew in the wild at about the same rate as the uncaged pinks on the tiles (Table 1). Although only 10 green abalones smaller than 100 mm survived to be measured after a year on the seabed, their growth rates were about the same whether they were in cages, on tiles, or released on natural substrate, and all were similar to the rates in the laboratory (Table 1).

Larger pinks, greens, and whites grew slower than smaller ones in all treatments (Table 2). (Complete data on growth of each individual, with graphs of growth increment vs. initial size for each treatment, are given in TUTSCHULTE, 1976.) The only instance in which this relationship differed among treatments was with white abalones (Table 2), owing to the fact that, in the field, only large individuals were observed. The values of the growth coefficients and asymptotic sizes, calculated with equation (2) from the data on observations of marked individuals, are given in Table 3.

Growth Rates Derived from Size-Frequency Data

The analyses of polymodal size frequencies of collections of pink abalones in the summers of 1971 and 1972 yielded the results shown in Figure 1. Because these two pooled samples were very large, we were able to use this method for size frequencies up to approximately 150 mm. Analyses of two larger samples (n = 1881 and n = 1822) from the pink population at Santa Cruz Island taken in March 1975 yielded very similar results (TUTSCHULTE, 1976, ap-

Table 1

Annual growth rates expressed as shell length increment in mm of small and large abalones (pinks, *Haliotis corrugata*; greens, *H. fulgens*; whites, *H. sorenseni*). Values are mean/SD (n).

Treatment	Pinks: initial length (mm)		Greens: initial length (mm)		Whites: initial length (mm)	
	<100	≥100	<100	≥100	<100	≥100
1. Held in laboratory	11.5/6.5 (175)	8.0/6.6 (13)	13.6/6.0 (24)	—	25.1/11.7 (10)	9.9/6.6 (9)
2. On tiles on the seabed at 9 m depth	14.8/3.6 (7)	3.9/2.9 (26)	13.6/2.9 (3)	4.0/2.4 (15)	—	1.7/1.8 (17)
3. On tiles on the seabed at 20 m depth	—	0.5/0.8 (35)	—	0.1/0.3 (19)	—	1.3/1.7 (15)
4. Caged on seabed at 9 m depth	11.7/4.8 (25)	—	13.0/7.7 (5)	7.0 (1)	—	—
5. Marked, released in wild for 1 yr at 5 m depth	16.4/7.1 (16)	—	13.0/9.2 (2)	—	—	—
6. Derived from size frequencies	16.4	—	16.0	—	23.3	—

Details of dates and initial sizes given in TUTSCHULTE, 1976.

Table 2

Growth increment vs. initial size; tests of whether the slopes of regressions were significant and equal among the treatments given in Table 1.

A. Pink abalones

1) *Analysis of covariance*

Source	df	Mean square	*F*	*P*
Initial size	1	2334.25	68.27	0.0001
Treatment	3	58.19	1.70	0.17
Size × treatment	3	77.95	2.28	0.08
Error	254	34.19		

2) *Mean values*

Treatment	Depth (m)	Mean annual growth increment (mm)	Mean initial size
1. Laboratory	—	11.27	55.4
2. Tiles on seabed	9	6.36	109.6
4. Caged on seabed	9	11.72	39.2
5. Released in wild	5	16.44	31.8

B. Green abalones*

1) *Analysis of covariance*

Source	df	Mean square	*F*	*P*
Initial size	1	1047.82	48.89	0.0001
Treatment	2	27.38	1.28	0.29
Size × treatment	2	53.89	2.51	0.09
Error	41	21.43		

2) *Mean values*

Treatment	Depth (m)	Mean annual growth increment (mm)	Mean initial size
1. Laboratory	—	13.5	53.8
2. Tiles on seabed	9	5.6	113.8
4. Caged on seabed	9	13.0	33.3

C. White abalones

1) *Analysis of covariance*

Source	df	Mean square	*F*	*P*
Initial size	1	2301.29	35.14	0.0001
Treatment	1	630.48	9.63	0.0040
Size × treatment	1	63.25	0.97	0.3331
Error	32	65.49		

Table 2

Continued.

2) *Mean values*

Treatment	Depth (m)	Mean annual growth increment (mm)	Mean initial size
1. Laboratory	—	17.89	85.79
3. Tiles on seabed	9	1.67	135.77

* For green abalones, the treatment "released in wild" had only two individuals, so was not included in this analysis.

pendix fig. 1). Both samples show that up to about 70 mm shell length (age 4 yr), growth rate is approximately linear at 16.4 mm/yr, but declines progressively thereafter. A von Bertalanffy curve was fitted for growth of pinks (Figure 1). The growth coefficient and asymptotic sizes are given in Table 3. As can be seen, they are similar to those calculated from equation (2) with the exception of the one based on individuals from the sea floor, which had a smaller asymptotic size.

The results of the polymodal frequency analyses of the green population samples are given in Figure 2. These data suggest that growth in length of green abalones is approximately linear over the first 6 yr at a rate of about 16.0 mm/yr. These samples were too small to use a polymodal analysis for sizes above 100 mm. Therefore, since the growth of pink abalones appears to be closely approximated by a von Bertalanffy curve after they reach sexual maturity (Figure 1), we have assumed the growth of green abalones follows the same pattern and have fitted a von Bertalanffy curve for growth (Figure 2). The growth coefficient and asymptotic size are given in Table 3; they agree well with those calculated from direct observations of marked individuals.

For white abalones, large samples are difficult to obtain since the population lives at greater depths than the other species. Because data on this species are scarce, we present an analysis of two small samples collected during search dives at a depth of 33 m in late November of 1971 and 1972. All spawning in the white population at Santa Catalina Island occurred in one short period, in March for the three preceding years (Tutschulte & Connell, 1981). Assuming that average annual growth rates do not vary among years, we grouped the size data as shown in Table 4. If the mean values of each group are plotted against the age estimates we have attributed to them, the results are consistent with a linear growth rate for the first 5 yr that is nearly double those of pinks and greens and very similar to the rate observed for whites in the laboratory (Table 1). The limited data indicate that older whites grow slower. A von Bertalanffy curve was fitted for growth (Figure 3).

Table 3

Calculated values of growth coefficients, asymptotic sizes, and age at 1 mm less than the asymptotic size, for three species of abalones. The laboratory and sea-floor data are from direct observations of marked individuals.

Species	Source of data	von Bertalanffy growth coefficient n	von Bertalanffy growth coefficient K	Asymptotic size L_∞ (mm)	Age at (L_∞ − 1.0 mm) yr
A. Ford model (equation 2)					
Pinks	Laboratory	188	0.080	201	57.6
Pinks	Sea floor, 5 & 9 m	74	0.109	169	40.7
Pinks	Size frequencies, 1971	15	0.090	185	50.3
Pinks	Size frequencies, 1972	14	0.089	184	50.8
Greens	Sea floor	26	0.092	179	48.8
Whites	Laboratory	19	0.142	221	33.1
B. von Bertalanffy model (equation 1)*					
Pinks	Size frequencies, 1971	509	0.097	202	54.5
Pinks	Size frequencies, 1972	685	0.098	202	54.1
Greens	Size frequencies, 1970–1972	24	0.101	205	52.9
Whites	Size frequencies, 1971–1972	13	0.152	210	35.0

* For the von Bertalanffy model, asymptotic size was taken as the largest individual found.

The growth coefficient and asymptotic size are given in Table 3; they agree well with those calculated from direct observations of marked individuals. From the different sets of data, the average ages at which these abalones would reach lengths within 1 mm of maximum were calculated, using equation (4). They are about 34 yr for whites and about 50 yr for pinks and greens (Table 3).

Variations in Growth Rates by Season

Average growth rates for periods of about 3 months for pinks caged at 9 m depth varied by a factor of four, with the highest value in spring and early summer (April to July) followed by the lowest rate in late summer and autumn (July to November), as shown in Tables 5 and 6. Lower rates were also shown in the other seasons by both this group and a second group of pinks at 2 m. Green abalones in the cages at 9 m depth showed seasonal average growth rates that varied six-fold, from a low value in the late winter (January to April) to a high rate in the late summer/autumn (July to October). The group of greens held at 2 m depth grew at about the same rate as those caged at 9 m in the same season. All seasonal variations were statistically significant (Table 6).

In the laboratory, similar patterns of seasonal variations in growth rates were shown by pinks (faster in spring–summer, slower in autumn–winter), but greens grew fastest in winter–spring and slowest in summer (Table 7). Whites held in the laboratory also exhibited a seasonal growth pattern, most rapid in winter–spring and slowest in autumn. Thus, each species had a different season of maximum growth: pinks in spring to early summer, greens in late summer to winter, and whites in spring.

To test the hypothesis that a shift in energy allocation into reproduction causes a reduction in growth, the growth rate during the season of most rapid gonad enlargement was compared to that in the preceding and following seasons. If the hypothesis is correct, growth of adults should be significantly less in the reproductive season than in the other seasons. Juveniles, on the other hand, should not show this pattern. Sufficient data exist only for pink abalones in the laboratory; pinks mature at 40 to 50 mm length, and gonads enlarge in the autumn (Tutschulte & Connell, 1981). Table 7 shows that growth in individual adult pink abalones was significantly less in autumn than in the preceding summer or the following winter. Juvenile growth decreased between summer and autumn but did not increase the next winter. These data are consistent with the hypothesis of a shift in energy allocation from growth into reproduction during the season of rapid gonad enlargement in adult pink abalones.

Variations of Growth with Depth

Pinks and greens in shallow water (less than 10 m depth) appear to grow at about the same average annual rates (Table 1). In an experiment in which large greens and pinks collected from a 5- to 7-m depth band were transplanted to an artificial habitat at 20 m, the pinks grew slowly at this much greater depth, while the greens did not grow at all (Table 1). In fact, the few greens that survived this transplant for 4 yr lost more than one-half of their body weight over a 2-yr period (Tutschulte, 1976). This is probably related to the lower temperatures and the decreased abundance of food at greater depths (Tutschulte & Connell, in press).

Large whites transplanted to artificial substrates at 9 m grew much slower than pinks and greens of similar size; some actually decreased in length (Table 1). Yet whites brought into the laboratory (equivalent in some respects

Table 4

Growth rates of white abalones from size frequencies (mm) grouped by eye. Collections from 33 m depth, November 1971 and November 1972.

Year class	Estimated age (yr)*	Observed shell length	Mean/SD shell length of class	Estimated annual growth rate
0	0.7	11.0		
		17.5		
		23.5	17.3/6.3	23.1†
1	1.7	40.5		
		46.5	43.5/4.2	26.2
2	2.7	55.5		
		63.0		
		63.0		
		65.0	61.6/4.2	18.1
3	3.7	77.0		
		81.0		
		95.0		
		96.0	87.3/9.7	25.7
4	4.7	112.0		
		113.0		
		114.0	113.0/1.0	25.7
5	5.7	120.0		
		122.0		
		126.0		
		126.0	123.5/3.0	10.5
6	6.7	132.0	—	8.5
7	7.7	145.0	—	13.0
8	8.7	155.0	—	10.0

* The white population in the Isthmus area of Santa Catalina Island spawned only in March during each of the four years of this study, 1970–1973 (TUTSCHULTE & CONNELL, 1981). Hence, whites of the zero-year age class were assumed to be 0.7 yr old in November, those of the 1-yr age class were assumed to be 1.7 yr old and so on.

† The annual rate for the zero-year class was calculated by assuming the growth rate was linear in the first year and adding 33% to the calculated mean length of the 0.7 yr old group.

to being transplanted to the shallow subtidal zone) grew much faster than pinks and greens under the same conditions. Whites placed on tiles at their natural depth of 20 m also grew very slowly. We offer the following explanation for this apparent anomaly.

The shell of an abalone is elongated along the anterior-posterior axis and most of the shell enlargement takes place by adding to the anterior end and to a lesser extent to the right side (see POORE, 1972, for detailed description). If this process takes place on a convex surface (the substrate where many large white abalones live), the margin of the shell aperture will not lie in a plane, as the margin of an oval platter does. When such a shell is placed on a flat surface, it will rest on the anterior and posterior ends with gaps on either side. Abalones rotate their shells up to 180° many times each day, grinding down the irregularities of the shell margin relative to the substrate. Thus, when transplanted to flat abrasive surfaces, such as the tiles used in these experiments, this behavior will abrade away the anterior and posterior ends. Whites have a much thinner shell than either pinks or greens, so that whites that had grown on a convex substrate would probably lose material from the anterior margin of the shell more rapidly and to a greater extent than either greens or pinks. In nature, the latter two species live mainly in cracks and crevices on flat surfaces, so the margin of their shell aperture tends to lie in a plane. Thus, pinks and greens placed on tiles will not wear away the anterior shell margin in the same manner as do whites. This loss in whites did not happen in the laboratory experiments, since the aquaria were made of acrylic or polyethylene plastic, both of which are softer than abalone shell.

Growth in Weight

Changes in body weight may or may not parallel those in shell length. To investigate growth in weight, we constructed a relationship between the logarithms of wet soft-body weight (without shell) and shell length, using measurements from large numbers of animals collected for reproductive assays. These variables are very highly correlated for each of the three species, as shown in Table 8. Using these equations the growth in weight for each species was calculated. As indicated by TUTSCHULTE (1976), the observed rates and the von Bertalanffy curves of relative weight change show that the rate of relative weight increase is highest for the smallest individuals and declines gradually with size. There is no abrupt discontinuity in the rate of decline at sexual maturity, which occurs at age 3 to 4 yr in pinks, 4 to 5 yr in whites and 6 yr in greens (TUTSCHULTE & CONNELL, 1981).

DISCUSSION

Our direct observations of growth rates for marked pink and green abalones agree closely for all treatments within species at the shallower depths and in the laboratory. When these species were transplanted to greater depths, and when large white abalones were transplanted from natural convex substrates to hard artificial ones, rates were lower. Since the former rates agreed among treatments and were similar to those based upon polymodal size-frequency analyses, we are inclined to accept them as reasonable estimates of growth of these three species at Santa Catalina Island.

The approximately linear juvenile growth rates described here for pink, green, and white abalones are similar to those reported for *Haliotis discus hannai* Ino (SAKAI, 1962), *H. tuberculata* L. (FORSTER, 1967), *H. midae* L. (NEWMAN, 1968), *H. rufescens* Swainson (LEIGHTON, 1968), *H. iris* Martyn (POORE, 1972), and *H. laevigata* Donovan (SHEPHERD & HEARN, 1983). Growth rates apparently slow down after age 3 to 5 yr.

The maximum lengths of these abalones range from about 100 mm for *Haliotis tuberculata* (FORSTER, 1967) to more than 280 mm for *H. rufescens* (COX, 1962). The largest individuals that we collected were much smaller

Table 5

Seasonal variations in shell growth rates of abalones held in the field in cages at two depths.

	Late summer/ autumn	Early winter	Late winter/ spring	Spring/ summer	Late summer/ autumn	Early winter
	Inclusive dates					
	24/VII/70 to 16/X/70	16/X/70 to 8/I/71	8/I/71 to 14/IV/71	14/IV/71 to 23/VII/71	23/VII/71 to 11/XI/71	20/XI/70 to 20/II/71
Interval (days)	84	84	96	100	111	92
	Pinks (9 m depth)					Pinks (2 m depth)
n	15	25	25	25	25	24
Mean initial length (mm)	37.7	39.2	40.8	43.7	49.4	37.8
Mean growth rate (mm/100 days)	2.11	2.02	3.08	5.70	1.44	2.20
	Greens (9 m depth)					Greens (2 m depth)
n	4	5	5	5	5	19
Mean initial length (mm)	39.5	33.3	34.2	35.1	39.9	39.8
Mean growth rate (mm/100 days)	6.13	1.43	0.94	4.80	5.77	1.50

than the 254-mm (10-inch) maximum that Cox (1962) listed for these three abalones. The asymptotic sizes we calculated (Table 3) were, in all but one case, quite similar to the largest individuals we collected.

The annual growth rates we report here for pink, green, and white abalones fall within the range of growth rates reported for other abalone species of similar maximum sizes with the exception of that of Shepherd & Hearn (1983). All but one of the abalone growth studies we have cited report annual rates of 15 to 30 mm for the first few years, followed by a progressive decline in annual growth rates. Only Shepherd & Hearn (1983) report significantly faster growth rates: first year growth of 40 to 50 mm followed by 32 and 29 mm in the second and third years for *Haliotis laevigata*.

The uniquely high rate of growth in the first year reported by Shepherd & Hearn (1983) was estimated by projecting the mean weekly growth rate of 0.9 mm for a group of 14- to 20-mm juveniles back to settlement. Thus, they estimated abalones 10 mm long to be about 11 weeks old. However, detailed measurements of young abalones indicate that their growth curve continually accelerates during early life. For example, Poore (1972) with *Haliotis iris* and Shepherd *et al.* (1985) with *H. scalaris* Leach found such a pattern. Likewise, white abalones reared in the laboratory by Leighton (1972, 1974) averaged 13.4 mm at the age of 1 yr, whereas we found laboratory growth of 1- to 3-year-olds of 25.1 mm/yr. Thus, the abalones measured by Shepherd & Hearn (1983) were probably still in the phase of accelerating growth rate when measured. If so, a linear extrapolation back to settlement would underestimate age and thus overestimate average growth rate. Whether the unusually high growth rates of Shepherd & Hearn (1983) indicate true rates, or possibly are overestimates, requires further investigation.

Good evidence exists (*e.g.*, Crisp & Patel, 1961; LeCren, 1962; Murdoch, 1966) for the claim that the cost of reproduction may reduce growth and survival of some organisms. Thus, the generalization that the processes of growth, maintenance, and reproduction compete for the organism's limited energy resources (Connell & Orias, 1964; Gadgil & Bossert, 1970) may apply to abalones. Tutschulte (1976) showed that both the total amount of gonadal material produced each year and its ratio to body-weight increment steadily increased following sexual maturity.

The hypothesis that a shift in energy allocation into reproduction causes a reduction in growth is supported by some but not all of the evidence in this study. Growth does

Table 6

Analysis of variance of seasonal growth of abalones shown in Table 5, using the data for the last four seasons at 9 m depth.

Source	df	Mean square	*F*	*P*
1. Pink abalones				
Seasons	3	90.30	30.00	0.0001
Individuals	24	5.67	1.88	>0.10
Error	72			
2. Green abalones				
Seasons	3	36.71	11.21	0.02
Individuals	4	13.43	4.10	0.10
Error	12			

Table 7

Seasonal variation in growth rates of abalones held in the laboratory. Values are the increment/100 days, given as the mean/SD (n).

Season	Pinks		Whites		Greens:
	Immature, <50 mm	Mature, ≥50 mm	Immature, <100 mm	Mature, ≥100 mm	immature, <100 mm
Winter/spring: 20 Dec 72–18 June 73	—	4.72/1.87 (3)	17.50/1.13 (3)	5.68/3.65 (4)	7.06/1.73 (2)
Spring: 10 March–18 June 73	8.67/1.44 (14)	6.80/1.13 (2)	—	—	—
Summer: 18 June–2 Oct 73	7.06/1.48 (12) **	5.57/1.57 (5) **	8.16/1.67 (2)	5.43/0.50 (3)	2.88/0.06 (2)
Autumn: 2 Oct 73–2 Jan 74	3.87/1.67 (11) ns	1.60/1.53 (6) **	3.07/0.06 (3)	0.45/0.79 (6)	4.80/2.16 (16)
Winter: 2 Jan–11 Apr 74	3.25/1.89 (10)	3.03/2.70 (6)	4.13/1.12 (3)	2.57/1.90 (3)	5.48/1.69 (16)

Comparisons of growth rates of individual pink abalones between certain pairs of seasons were made using the Wilcoxon matched-pairs signed ranks test. The results are indicated as ** $0.01 > P > 0.001$ and ns = $P > 0.05$.

slow down in older abalones, but not abruptly at the age of sexual maturity (Figures 1–3). However, as shown in Table 7, the growth of adult pink abalone was significantly less in the autumn, when gonads rapidly enlarge, than in the preceding summer or following winter. Since the juveniles also decrease in growth from summer to autumn, this seasonal reduction could be explained by reductions in temperature or by unknown other environmental changes. However, the fact that the growth of adults then increases in winter, whereas that of juveniles remains low, suggests that, once gonads have ceased enlarging in the late autumn, energy is again allocated to shell and somatic body growth in adults.

Forster (1967) stated that the size at which growth decreased coincided with that of sexual maturity in *Haliotis tuberculata*. Paul *et al.* (1977) found that sexually mature *H. kamtschatkana* Jones held in the laboratory did not grow during the 90 days preceding spawning, then grew rapidly during the following 90 days. Shepherd & Hearn (1983) reported that for both *H. laevigata* and *H. ruber* Leach, in a location where sea temperature varies little and the food supply seems abundant all year, the period of gonad production coincides with a lower growth rate. In summary, some analyses of seasonal variations in growth and gonad production in abalones support the hypothesis that the cost of reproduction reduces growth.

Table 8

Weight-length relationships of pink, green, and white abalones. Regression of wet soft-body weight in grams on shell length in mm, using natural logarithms for both length and weight.

Species	n	Slope	Intercept	r	P
Pink	100	3.23	−10.46	0.996	≪0.01
Green	86	3.38	−11.12	0.996	≪0.01
White	109	4.02	−14.51	0.929	≪0.01

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LITERATURE CITED

Bertalanffy, L. von. 1934. Untersuchungen über die Gasetzlichkeit des Wachstums. 1. Arch. Entwicklungsmech. Organ. 131:613.

Bertalanffy, L. von. 1938. A quantitative theory of organic growth (inquiries on growth laws. 11). Human Biology 10: 181–213.

Bertalanffy, L. von. 1960. Principles and theory of growth. Pp. 137–359. *In:* W. W. Nowinski (ed.), Fundamental aspects of normal and malignant growth. Elsevier: Amsterdam.

Beverton, R. H. J. 1954. Notes on the use of theoretical models in the study of the dynamics of exploited fish populations. U.S. Fish. Lab., Beaufort, North Carolina, Misc. Contrib. 2:159.

BEVERTON, R. H. J. & S. J. HOLT. 1957. On the dynamics of exploited fish populations. Great Brit. Min. Agr. Fish., Fish. Invest., Ser. 2, 19:1–533.

BRODY, S. 1927. Growth rates. Univ. Missouri Agric. Exp. Sta. Bull. 97.

CASSIE, R. M. 1950. The analysis of polymodal frequency distributions by the probability paper method. N.Z. Sci. Rev. 8:89–91.

CASSIE, R. M. 1954. Some uses of probability paper in the analysis of size frequency distributions. Austral. Jour. Mar. Freshwater Res. 5:513–533.

CONNELL, J. H. & E. ORIAS. 1964. The ecological regulation of species diversity. Amer. Natur. 98:399–414.

COX, K. W. 1962. California abalones, family Haliotidae. Fish Bull., California, No. 118.

CRISP, D. J. & B. PATEL. 1961. The interaction between breeding and growth rate in the barnacle *Elminius modestus* Darwin. Limnol. Oceanogr. 6:105–115.

CROFTS, D. R. 1929. *Haliotis*. Liverpool Mar. Biol. Comm., Mem. No. 29.

EBERT, T. A. 1973. Estimating growth and mortality rates from size data. Oecologia 11:281–298.

EBERT, T. A. 1975. Growth and mortality of post-larval echinoids. Amer. Zool. 15:755–775.

EBERT, T. A. 1980. Estimating parameters in a flexible growth equation, the Richards function. Can. Jour. Fish. Aquat. Sci. 37:687–692.

FABENS, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289.

FORD, E. 1933. An account of the herring investigations conducted at Plymouth during the years from 1924–1933. Jour. Mar. Biol. Assoc. U.K. 19:305–384.

FORSTER, G. R. 1967. The growth of *Haliotis tuberculata*: results of tagging experiments in Guernsey 1963–65. Jour. Mar. Biol. Assoc. U.K. 47:287–300.

FOURNIER, D. A. & P. A. BREEN. 1983. Estimation of abalone mortality rates with growth analysis. Trans. Amer. Fish. Soc. 112:403–411.

GADGIL, M. & W. H. BOSSERT. 1970. Life historical consequences of natural selection. Amer. Natur. 104:1–24.

GREEN, R. H. 1970. Graphical estimates of rates of mortality and growth. Jour. Fish. Res. Bd. Can. 27:204–208.

HARDING, J. P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. Jour. Mar. Biol. Assoc. U.K. 28:141–153.

HASSELBLAD, V. 1966. Estimation of parameters for a mixture of normal distributions. Technometrics 8:431–444.

HAYASHI, I. 1980. Structure and growth of a shore population of the ormer, *Haliotis tuberculata*. Jour. Mar. Biol. Assoc. U.K. 60:431–437.

LECREN, E. D. 1962. The efficiency of reproduction and recruitment in freshwater fishes. Pp. 283–296. *In:* E. D. LeCren & M. W. Holgate (eds.), The exploitation of natural animal populations. Blackwell: Oxford.

LEIGHTON, D. L. 1968. A comparative study of food selection and nutrition in the abalone, *Haliotis rufescens* (Swainson) and the sea urchin, *Strongylocentrotus purpuratus* (Stimpson). Ph.D. Dissertation, University of California, San Diego.

LEIGHTON, D. L. 1972. Laboratory observations on the early growth of the abalone, *Haliotis sorenseni*, and the effect of temperature on larval development and settling success. Fish. Bull. 70:373–381.

LEIGHTON, D. L. 1974. The influence of temperature on larval and juvenile growth in three species of southern California abalones. Fish. Bull. 72:1137–1145.

MACDONALD, P. D. M. & T. J. PITCHER. 1979. Age-groups from size-frequency data: a versatile and efficient method for analyzing distribution mixtures. Jour. Fish. Res. Board Can. 36:987–1001.

MCNEW, R. W. & R. C. SUMMERFELT. 1978. Evaluation of a maximum-likelihood estimator for analysis of length-frequency distributions. Trans. Amer. Fish. Soc. 107:730–736.

MURDOCH, W. W. 1966. Population stability and life history phenomena. Amer. Natur. 100:5–11.

NEWMAN, G. G. 1968. Growth of the South African abalone, *Haliotis midae*. Div. Sea Fish. S. Afr., Invest. Rep. No. 67.

PAUL, A. J., J. M. PAUL, D. W. HOOD & R. A. NEVE. 1977. Observations on food preferences, daily ration requirements and growth of *Haliotis kamtschatkana* Jonas in captivity. Veliger 19:303–309.

POORE, G. C. B. 1972. Ecology of New Zealand abalones, *Haliotis* species (Mollusca: Gastropoda) 3. Growth. N.Z. Jour. Mar. Freshwater Res. 6:534–559.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Bd. Can. Bull. 191:382 pp.

SAINSBURY, K. J. 1980. Effect of individual variability on the von Bertalanffy growth equation. Can. Jour. Fish. Aquat. Sci. 37:241–247.

SAINSBURY, K. J. 1982. Population dynamics and fishery management of the paua, *Haliotis iris* 1. Population structure, growth, reproduction and mortality. N.Z. Jour. Mar. Freshwater Res. 16:147–161.

SAKAI, S. 1962. Ecological studies on the abalone, *Haliotis discus hannai* Ino IV. Studies on the growth. Bull. Jap. Soc. Sci. Fish. 28:899–904.

SCHNUTE, J. & D. FOURNIER. 1980. A new approach to length-frequency analysis: growth structure. Can. Jour. Fish. Aquat. Sci. 37:1337–1351.

SHEPHERD, S. A., P. S. CLARKSON & J. A. TURNER. 1985. Studies on southern Australian abalone (genus *Haliotis*). V. Spawning, settlement and early growth of *H. scalaris*. Trans. Royal Soc. S. Austr. 109:61–62.

SHEPHERD, S. A. & W. S. HEARN. 1983. Studies on southern Australian abalone (genus *Haliotis*). IV. Growth of *H. laevigata* and *H. ruber*. Austr. Jour. Mar. Freshwater Res. 34: 461–475.

TUTSCHULTE, T. C. 1976. The comparative ecology of three sympatric abalones. Ph.D. Dissertation, University of California, San Diego.

TUTSCHULTE, T. C. & J. H. CONNELL. 1981. Reproductive biology of three species of abalone (*Haliotis*) in southern California. Veliger 23:195–206.

TUTSCHULTE, T. C. & J. H. CONNELL. In press. Feeding behavior and the distribution, abundance and productivity of algal food of three species of abalones (*Haliotis*) in southern California. Mar. Ecol. Prog. Ser.

WALFORD, L. A. 1946. A new graphic method of describing the growth of animals. Biol. Bull. 90:141–147.

YONG, M. Y. Y. & R. A. SKILLMAN. 1975. A computer program for analysis of polymodal frequency distributions (ENORMSEP), FORTRAN IV. Fish. Bull. 73:681.

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Random Mating and Planktotrophic Larval Development in the Brooding Hermaphroditic Clam *Lasaea australis* (Lamarck, 1818)

by

DIARMAID Ó FOIGHIL[1]

Friday Harbor Laboratories, Friday Harbor, Washington 98250, U.S.A.

Abstract. *Lasaea australis* differs markedly from congeners in important details of its early ontogeny and reproduction. Adults brood their young to a straight-hinged veliger stage and an obligate planktotrophic larval period precedes settlement and metamorphosis. Several lines of evidence indicate that *L. australis* reproduces primarily by cross-fertilization. These include the maintenance of a Hardy-Weinberg-Castle equilibrium, and an observed heterozygosity level of 0.635, at the highly polymorphic glucose-6-phosphate isomerase locus. In addition, *L. australis* appears to be an alternate sequential hermaphrodite and has a large male allocation (approximately 50% in terms of gonadal volume). These results are the first to provide evidence of amphimixis in *Lasaea*. A profound dichotomy exists within the genus in developmental and reproductive modes, and population genetic structure. *Lasaea australis* probably represents the ancestral condition, and congeners that lack a planktonic larva form a complex assemblage of uncertain taxonomic status.

INTRODUCTION

The galeommatacean bivalve genus *Lasaea* is known from the Eocene period and has attained a near-cosmopolitan distribution (Chavan, 1969). *Lasaea* are small (≤6 mm in valve length) crevice dwellers, found in the rocky intertidal within cracks, algal holdfasts, barnacle test interstices, lichen tufts, and under rocks (Keen, 1938; Morton, 1954; Morton *et al.*, 1957; Oldfield, 1964; Glynn, 1965; Ponder 1971; Booth, 1979; Seed & O'Connor, 1980; Crisp *et al.*, 1983; Roberts, 1984; Beauchamp, 1986; McGrath & Ó Foighil, 1987). Although *Lasaea* is one of the better studied and most readily sampled marine bivalves, its taxonomy and some aspects of its reproduction are subject to conflicting interpretations.

Bivalve systematists have traditionally relied heavily on shell morphology to distinguish between species. There is much individual variation in *Lasaea* shells (Dall, 1900; Ponder, 1971; Roberts, 1984; Ó Foighil, 1986a; Ó Foighil & Eernisse, in press) and this poses a difficult taxonomic dilemma. Keen (1938) lists >40 species distinguished from each other on the basis of slight differences in shell morphology and color. A number of more recent workers, however, have been unable to separate many of these nominal *Lasaea* species (Soot-Ryen, 1960; Dell, 1964; Barnard, 1964; Ponder, 1971; Haderlie & Abbott, 1980; Beauchamp, 1985). An extreme alternative view is that the genus is monospecific (Dall, 1900; Lamy, 1906; Dautzenberg, 1929). Ponder (1971) concluded that many of the nominal *Lasaea* species are merely regional subspecies or ecotypes of the type species *Lasaea rubra* (Montagu, 1803). However, he distinguished two additional species, *L. australis* (Lamarck, 1818) and *L. maoria* (Powell, 1933), on the basis of shell and soft part morphology.

Population genetic studies of *Lasaea* in Europe (Crisp *et al.*, 1983) and the northeastern Pacific (Ó Foighil, 1986a; Ó Foighil & Eernisse, in press) have revealed the existence of a variety of non-hybridizing, frequently sympatric, genetic strains. These results have important implications for understanding morphological variation and systematic relationships within the genus. Crisp *et al.* (1983) concluded that the populations they examined were composed of female, apomictic clones. They apparently overlooked an earlier detailed study (Oldfield, 1961) which

[1] Present address: Biology Department, University of Victoria, P.O. Box 1700, Victoria, British Columbia, Canada V8W 2Y2.

described European *Lasaea* as simultaneous hermaphrodites with greatly reduced male allocation, recently confirmed by McGrath & Ó Foighil (1986). Ó Foighil & Eernisse (in press) consider that northeastern Pacific *Lasaea* strains are either products of prolonged autogamy (self-fertilization), or pseudogamy in association with meiotic parthenogenesis.

Galeommatacean species investigated to date brood their young, either to a straight-hinged veliger (Chanley & Chanley, 1970; Ó Foighil & Gibson, 1984) or to a crawl-away juvenile stage of development (Gage, 1979). *Lasaea* developmental modes have been determined in European (Oldfield, 1964; Seed & O'Connor, 1980; McGrath & Ó Foighil, 1986), Ascension Island (Rosewater, 1975), New Zealand (Booth, 1979), Hawaiian (Kay, 1979) and northeastern Pacific (Glynn, 1965; Ó Foighil, 1986; Beauchamp, 1986) populations. In all of these cases, offspring are released as crawl-away juveniles. There are indications, however, that *L. australis,* which occurs around the Australian continent (Dell, 1964), may differ from its congeners in its developmental mode. Ponder (1971) reports that *L. australis* has a smaller prodissoconch (approximately 200 μm in length) relative to other *Lasaea* (500–600 μm). Prodissoconch size is directly related to egg size and developmental mode in eulamellibranch bivalves (Ockelmann, 1965; Waller, 1981; Jablonski & Lutz, 1983). The smaller *L. australis* prodissoconch is indicative of a shorter brooding period, possibly involving an obligate planktonic larval state. Roberts (1984) investigated the reproductive cycle of *L. australis* in Western Australia and described it as being larviparous, without reporting the developmental stage when released from the parent, egg size, or brood number. *Lasaea* that retain their young to a juvenile stage of development have also been frequently described as brooding "larvae" (Booth, 1979; Kay, 1979). Confirmation that *L. australis* does indeed differ in its developmental mode from other *Lasaea* is important because developmental modes exert a profound influence on population genetic composition and consequently on the evolution of reproductive patterns (Charlesworth & Charlesworth, 1981; Strathmann *et al.,* 1984; Lande & Schemske, 1985). Though there is yet no evidence for cross-fertilization in this genus, a reproductive mode involving an obligate larval dispersal is likely to result in high population genetic diversity (Berger, 1983) which would form a potent genetic penalty for self-fertilizers in the form of a pronounced inbreeding depression (Maynard Smith, 1978). Accordingly, an obligate planktonic larval period in *L. australis* should select for a predominantly cross-fertilizing reproductive mode.

The aim of this study is to assess the systematic status of *Lasaea australis* within this unusual genus by characterizing its developmental and reproductive modes. A live sample was obtained (courtesy of W. F. Ponder, Australian Museum), from which the hinge structure, duration of brood care, sex allocation, and population genetic structure at a polymorphic isozyme locus were determined.

MATERIALS AND METHODS

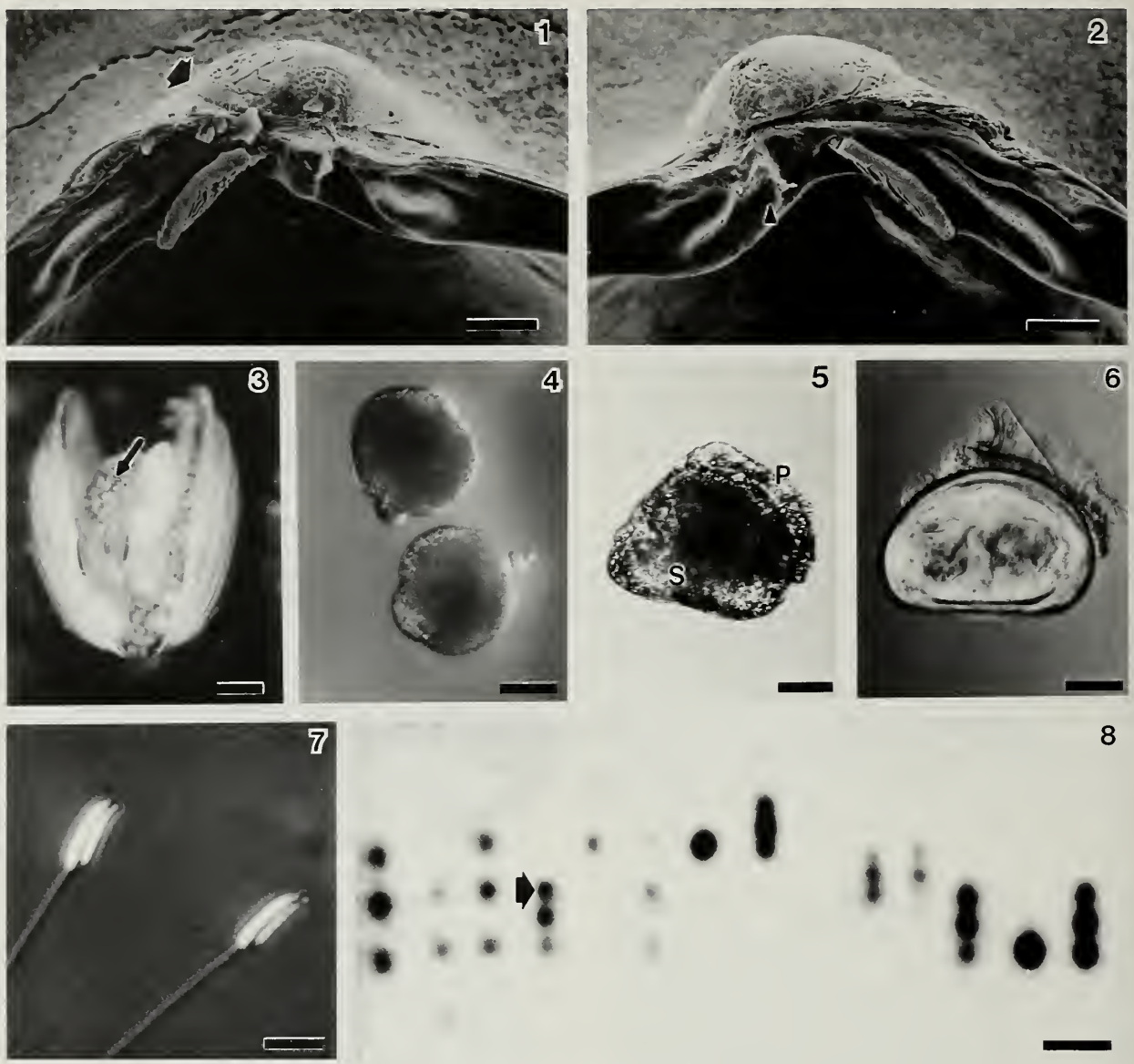
One hundred and five specimens of *Lasaea australis* were sampled in August 1987 from the intertidal zone at Long Reef, New South Wales, Australia (33°44′S, 151°18′E) by P. H. Colman. They were heat-sealed in a plastic bag containing approximately 50 mL of seawater, were air mailed, and arrived at the Friday Harbor Laboratories 10 days later. All specimens survived the trip; indeed, many had spawned en route and were brooding developing embryos upon arrival. They were maintained in seawater tanks at room temperature (18–20°C) and fed cultured *Thallassosira pseudonana* (strain 3H) for a week, then starved for one day before electrophoretic analysis.

Ninety-eight specimens were characterized electrophoretically using 13% starch gels and standard power supplies. Broods were dissected from reproducing individuals; the adults were then removed from their valves and homogenized with glass rods in an equal volume of gel buffer. A single discontinuous tris-citrate buffer system (electrode: 18.55 g boric acid and 2.4 g sodium hydroxide/L, pH 8.2; gel: 9.21 g tris and 1.05 g monohydrate citric acid/L, pH 8.7) was used. The following enzymes yielded monomorphic protein phenotypes: leucine amino peptidase, peptidase with glycyl-lycine, and peptidase with leucyl-valine and leucyl-tyrosine substrates. Glucose-6-phosphate isomerase (GPI; EC 5.3.1.9), however, produced closely migrating, polymorphic protein phenotypes, which were sufficiently resolved when gels were run at 200 volts until the front had reached a preset "destiny" of 130 mm. The GPI staining assay and method of scoring electromorph phenotypes of Tracey *et al.* (1975) were employed. Statistical analyses were performed using standard techniques as previously described (Ó Foighil & Eernisse, 1987).

Hinge structure of air-dried, gold-coated *Lasaea australis* valves was examined using a JOEL JSM-35 scanning electron microscope and compared with that of congeners from Victoria, B.C. (Canada), New Zealand (lots m. 21828 and m. 21011, National Museum of New Zealand), Japan (lot 78-14, Los Angeles County Museum of Natural History), Florida (lot PSM-743, Indian River Coastal Zone Museum), Britain (lot 35873, Museum of Zoology, University of Michigan), South Africa (lot A32355, South African Museum), and the Seychelles (lot 2222, British Museum of Natural History). Brooding individuals were photographed with a Wild Photomacroscope. Straight-hinged veliger larvae released by brooding parents were relaxed in 6.7% $MgCl_2$ at 4°C and fixed in 2% formaldehyde. Embryos, larvae, and sperm cells were photographed using Nomarski differential interference contrast optics on a Nikon Optiphot light microscope.

RESULTS

Figures 1 and 2 respectively show the hinge structure of the left and right valves of a *Lasaea australis* specimen 1.2 mm in valve length. The left hinge contains a single truncated anterior lateral tooth, a short thornlike cardinal (more



Explanation of Figures 1 to 8

Figure 1. Scanning electron micrograph (SEM) of left hinge of *Lasaea australis* specimen 1.2 mm in valve length. Arrow indicates prodissoconch-dissoconch boundary. Scale bar = 75 μm.

Figure 2. SEM of right valve of same *L. australis* specimen as in Figure 1. Arrow indicates small spur on posterior end of ventral anterior lateral tooth. Scale bar = 75 μm.

Figure 3. Light micrograph (LM) of a brooding *L. australis*, with opened valves, revealing brood mass (arrow) in the suprabranchial chamber. Scale bar = 0.5 mm.

Figure 4. Nomarski differential interference contrast (DIC) LM of *L. australis* eggs removed from the brood chamber just prior to first cleavage. Each egg bears polar bodies at the animal pole and a polar lobe at the vegetal pole. Scale bar = 40 μm.

Figure 5. Nomarski DIC LM of a *L. australis* larva dissected from the brood chamber at a late trochophore stage of development. Note developing shell (S) and faint prototroch (P). Scale bar = 30 μm.

Figure 6. Nomarski DIC LM of a *L. australis* straight-hinged veliger just after release from parent. The well-developed velum is partially retracted. Scale bar = 40 μm.

Figure 7. Nomarski DIC LM of *L. australis* sperm cells. Scale bar = 5 μm.

Figure 8. GPI electromorphs of 13 Long Reef *L. australis* individuals showing all five alleles detected in this study. Arrow indicates the modal allele (100). Scale bar = 10 mm and is placed anodally.

pronounced in larger specimens), an oblique resilium, and a lamellar posterior lateral tooth. In the right hinge, the short anterior lateral is bifurcate, forming a groove that accepts the left anterior lateral. In larger individuals this bifurcation is less evident and the ventral anterior lateral becomes much more pronounced, developing a spur at its posterior end which may represent a fused cardinal tooth (Figure 2). The right hinge also contains a pit which articulates with the left cardinal tooth, an oblique resilium, and two lamellar posterior laterals. The ventral posterior lateral is relatively more pronounced, and the groove separating the two laterals accepts the single posterior lateral of the left hinge. Shell shape, color, and sculpture are variable as previously found by PONDER (1971) and ROBERTS (1984). Individuals could be entirely white or pinkish-red in external valve coloration and many specimens had abruptly changed shell coloration during valve growth. Some individuals had heavy concentric folding on their external valve surfaces.

As in other *Lasaea,* developing young are retained in the suprabranchial chamber (Figure 3). The brood is held in both inner and outer demibranchs; the latter is reduced to one-third the size of the inner demibranch. Brood sizes of 440 and 2870 were produced by two individuals, 2.16 and 4.25 mm in respective valve lengths. *Lasaea australis* eggs are 90–95 μm in diameter and undergo two maturation divisions before first cleavage (Figure 4). Early development is similar to that found in other galeommatacean bivalves that retain their offspring to a straight-hinged veliger stage of development (Ó FOIGHIL & GIBSON, 1984). A shell is formed at the late trochophore stage and it gradually extends to cover a poorly developed prototroch (Figure 5). When released from the parent, the larvae are planktotrophic veligers (Figure 6) and have a mean length of 144 ± 3.9 μm SE ($n = 15$). *Lasaea australis* prodissoconch morphology is typical of bivalves with planktotrophic development (OCKELMANN, 1965; CARRIKER & PALMER, 1979; WALLER, 1981; JABLONSKI & LUTZ, 1983; Ó FOIGHIL, 1986b). Newly metamorphosed juveniles possess an umbonate hinge line, a small prodissoconch-I (130–150 μm in length) and have a mean length of 249 ± 19.6 μm SE ($n = 10$), based on prodissoconch-II measurements.

Specimens brooding early embryos did not retain any residual vitellogenic oocytes in the gonad and had obviously just spawned as females. However, the testes of these individuals were usually full of mature sperm (7 out of 9 cases). These data imply that *Lasaea subviridis* is a sequential alternate hermaphrodite, although observations of actual spawnings are necessary to confirm this. Male allocation in *L. australis* is considerable, being roughly equal to female allocation in terms of gonadal volume. *Lasaea australis* sperm morphology at the light microscope level conforms to the "primitive" sperm type found in most externally fertilizing aquatic organisms (FRANZÉN, 1956; AFZELIUS, 1972). The sperm heads contain a fully condensed nucleus and are uniform in shape and size (Figure 7).

Table 1

Allelic frequencies of Long Reef *Lasaea australis* at the GPI locus.

Allele	Frequency ± 1 SE
82	0.0306 ± 0.0123
92	0.3367 ± 0.0337
100	0.3673 ± 0.0344
108	0.2449 ± 0.0307
114	0.0306 ± 0.0123

Ne (effective number of alleles) = 3.225. Number of alleles screened = 196. Observed proportion of heterozygotes (Ho) = 0.653. Expected proportion of heterozygotes (He) = 0.690. D = −0.053 when D = (Ho − He)/He (SELANDER, 1970).

GPI electromorphs from the 98 individuals analyzed for this enzyme consisted of either one or three bands (Figure 8), indicating that this enzyme has a dimer subunit structure in *Lasaea australis*. The protein phenotype combinations observed are consistent with the hypothesis that five distinct alleles segregating through a single locus were distinguished. Therefore, single-banded individuals were assumed to be homozygous and three-banded animals heterozygous at the GPI locus. Allele frequencies and genotype distributions are presented in Tables 1 and 2 respectively. The calculated D value (SELANDER, 1970) of −0.053 is marginally less than the expected value of 0 and indicates that there is a slight deficiency of heterozygotes at the GPI locus. However, the observed allele combination frequencies do not differ significantly from random mating expectations ($0.75 < P < 0.9$).

DISCUSSION

Lasaea australis differs from all congeners studied to date in important features of its reproductive and developmental biology. The maintenance of a Hardy-Weinberg-Castle equilibrium at the GPI locus ($0.75 < P < 0.9$) indicates that random mating occurs in the Long Reef population and provides the first evidence for cross-fertilization in this genus. Occasional self-fertilization by *L. australis* cannot be excluded; however, the observed GPI locus heterozygosity level of 0.653 suggests that, if it occurs, it is a rare event. Frequent self-fertilization would lead to a rapid drop in heterozygosity at all loci in the genome (SELANDER & KAUFMAN, 1973; BELL, 1982; BUCKLIN *et al.*, 1984).

Additional evidence for an amphimictic reproductive mode is provided by the large male allocation, approximately 50% of gonad volume, which is theoretically consistent with an outcrossing reproductive mode (HEATH, 1979; FISCHER, 1981; CHARLESWORTH & CHARLESWORTH, 1981; CHARNOV, 1982). European (OLDFIELD, 1964; MCGRATH & Ó FOIGHIL, 1986) and northeastern Pacific (Ó FOIGHIL, 1985a; BEAUCHAMP, 1986) *Lasaea* populations are composed of simultaneous hermaphrodites, the male allocation of which is approximately an

Table 2

Genotype distributions of the three most common GPI alleles of Long Reef *Lasaea australis*.

Genotype	Observed frequency	H-W-C expected frequency
92/92	11	11.110
92/100	26	24.239
92/108	13	16.162
100/100	14	13.221
100/108	13	17.631
108/108	9	5.878

$G = 0.88387$, df = 3, $0.75 < P < 0.9$ when G is the Log Likelihood Ratio.

order of magnitude smaller than that of *L. australis*. Sperm morphology is also different in *L. australis* in that sperm nuclei are fully condensed, resulting in a sperm head that is uniform in size and form. In European and northeastern Pacific *Lasaea* populations the degree of sperm nuclear condensation and the sperm head size and shape are variable (Ó Foighil 1985a; McGrath & Ó Foighil, 1986).

Data from the present study on early development of *Lasaea australis* confirms Robert's (1984) description of this species as being larviparous. *Lasaea australis* differs in its developmental mode from congeners in Europe (Oldfield, 1964; Seed & O'Connor, 1980; McGrath & Ó Foighil, 1986), the northeastern Pacific (Glynn, 1965; Ó Foighil, 1986; Beauchamp, 1986), Ascension Island (Rosewater, 1975), New Zealand (Booth, 1979), and Hawaii (Kay, 1979) in that it releases its young as straight-hinged planktotrophic veligers rather than as crawl-away juveniles. *Lasaea australis* has a correspondingly smaller egg size, greater fecundity, and assumes a benthic juvenile existence at a smaller size than congeners (McGrath & Ó Foighil, 1986).

The hinge structure of *Lasaea australis* is very similar to that of congeners from Victoria, B.C. (Canada), New Zealand, Japan, Florida, Britain, South Africa, and the Seychelles. Congeners, however, exhibit great individual variation in the degree of tooth development, especially that of the anterior laterals (Ó Foighil, unpublished data). This variation is much less pronounced in *L. australis*. *Lasaea australis* is readily distinguished from congeners by its larger size (up to 6 mm in valve length), presence of heavy concentric ridges on the external shell surface of some individuals, and smaller prodissoconch (Ponder, 1971).

Electrophoretic characterization of European (Crisp *et al.*, 1983) and northeastern Pacific (Ó Foighil, 1986; Ó Foighil & Eernisse, unpublished data) populations has revealed a variety of non-hybridizing, sympatric strains to whom species rank cannot yet be assigned with certainty. The profound differences in reproduction, development, and population genetic structure between *Lasaea australis* and its congeners, in addition to shell characteristics (Ponder, 1971), justify its ranking as a distinct species.

Available data on the population genetic structure, reproduction, and development of *Lasaea* reveal a prominent dichotomy between *L. australis* and European/northeastern Pacific populations (Crisp *et al.*, 1983; Ó Foighil, 1986; Ó Foighil & Eernisse, in press). *Lasaea australis* is a randomly mating species with an obligate planktotrophic larval development. The other *Lasaea* populations are composed of frequently sympatric, reproductively isolated strains, with no evidence as yet for cross-fertilization, and brood to a crawl-away juvenile stage of development. This population genetic structure can result from a variety of reproductive modes, including prolonged autogamy and apomixis (Bell, 1982).

Northeastern Pacific *Lasaea* are simultaneous hermaphrodites (Glynn, 1965; Beauchamp, 1986) with minute male allocation, approximately 5% in terms of gonadal volume (Ó Foighil, 1985a), and are capable of reproducing in isolation, apparently by self-fertilization (Ó Foighil, 1987). Reduced male allocation in simultaneous hermaphrodites is a theoretical consequence of high degrees of autogamy (Heath, 1979; Fischer, 1981; Charlesworth & Charlesworth, 1981; Charnov, 1982). Indeed, the population genetic structure of northeastern Pacific *Lasaea*, together with the ability to reproduce in isolation, a minute male allocation, and an apparent absence of specialized sperm transfer mechanisms typically found in cross-fertilizing brooding bivalves (*e.g.*, spermatophores and spermatozeugma [Coe, 1931; Ockelmann & Muus, 1978; Ó Foighil, 1985b], dwarf and complemental males [Turner & Yakovlev, 1983; Ó Foighil, 1985c] and pseudocopulation [Townsley *et al.*, 1965]) imply that cross-fertilization may be a very rare event in northeastern Pacific *Lasaea* populations (Ó Foighil, 1986a; Ó Foighil & Eernisse, unpublished data). The conclusion that northeastern Pacific *Lasaea* reproduce predominantly by autogamy (Ó Foighil, 1986a, 1987; Ó Foighil & Eernisse, in press) is supported by the marked difference in their population genetic structure and male allocation to that of the predominantly amphimictic *L. australis*. An alternative, less parsimonious interpretation is that northeastern Pacific *Lasaea* engage in a combination of pseudogamy and meiotic parthenogenesis (Ó Foighil, 1987). An analysis of the degree of male and female pronuclear interaction is necessary to distinguish between these two possibilities. European *Lasaea* populations are very similar in population genetic structure, male allocation, and presumably reproductive mode to northeastern Pacific *Lasaea* (Oldfield, 1961; Crisp *et al.*, 1983; McGrath & Ó Foighil, 1986).

A strong unidirectional bias exists in the transition between feeding and non-feeding larval development in marine invertebrates because loss of planktotrophy is usually accompanied by an extensive loss of larval feeding structures (Strathmann, 1978, 1985). Oldfield (1964) in-

terpreted the unciliated "cephalic mass" of *Lasaea rubra* embryos as a velum highly modified for yolk storage. Similar, though less developed, modifications in velar morphology are found in *Thyasira gouldi* and *Cardiomya pectinata* which lack feeding larvae (BLACKNELL & ANSELL, 1974; GUSTAFSON *et al.*, 1986). It is probable that the *Lasaea australis* developmental mode represents the primitive condition in the genus.

Loss of a dispersive life-history stage gives rise to philopatric dispersal patterns which can result in prolonged inbreeding (JACQUARD, 1975). A history of inbreeding predisposes populations to the development of autogamy by removing recessive deleterious alleles (CHARLESWORTH & CHARLESWORTH, 1981; CHARNOV, 1982; STRATHMANN *et al.*, 1984; UYENOYAMA, 1986). Self-fertile hermaphrodites with reduced male allocation appearing in these populations are then at a reproductive advantage because of their greater reproductive efficiency (MAYNARD SMITH, 1978; CHARNOV, 1982; STRATHMANN *et al.*, 1984). The model of STRATHMANN *et al.* (1984) for the evolution of self-fertile hermaphrodites in marine invertebrate brooders that release crawl-away young may apply to all *Lasaea* populations that brood to this ontogenic stage. Once evolved, a completely self-fertilizing reproductive mode may be irreversible owing to a genetic advantage resulting from the "cost of meiosis" (BULL & CHARNOV, 1985).

Although amphimixis has for a long time been regarded as a preadaptation to variable conditions, comparative evidence shows that alternative reproductive mechanisms, including autogamy and apomixis, predominate in harsh and disturbed environments (BELL, 1982). The small size, physiological toughness, and behavioral adaptations of European (BALLANTINE & MORTON, 1956; MORTON *et al.*, 1957; MORTON, 1960; DAVENPORT & BEARD, 1988) and northeastern Pacific (GLYNN, 1965) *Lasaea* enable them to survive in their upper intertidal habitat. Prominent theories concerning the evolution and persistence of amphimixis, such as the Tangled Bank (BELL, 1982) and the Red Queen (JAENIKE, 1978; BELL, 1982), stress its role in generating the genetic diversity necessary to endure in, and more fully exploit, biologically diverse environments. *Lasaea australis* not only differs from its congeners in reproductive mode, but also in habitat, occurring in the more biologically complex lower intertidal zone (ROBERTS, 1984).

A profound taxonomic dichotomy exists in the genus *Lasaea* that may have evolved as follows. Originally, the genus was composed of amphimictic hermaphrodites with an obligate planktotrophic larval development. To date, the only species known to retain this presumably ancestral condition is *L. australis*. Loss of a planktonic larva in some species led to the successful development of a self-fertilizing reproductive mode. It is not yet certain if self-fertilization has been maintained in northeastern Pacific populations, or if it has been replaced by a form of pseudogamy in which endogenous sperm trigger meiotic parthenogenesis. The absence of amphimixis has resulted in the formation of a complex of non-hybridizing, often sympatric strains in at least northeastern Pacific (Ó FOIGHIL, 1986, Ó FOIGHIL & EERNISSE, in press) and probably in European (OLDFIELD, 1961; CRISP *et al.*, 1983; MCGRATH & Ó FOIGHIL, 1986) populations. Taxonomic relationships among *Lasaea* that lack a planktonic larva are still poorly understood, but are undoubtedly complex (PONDER, 1971; CRISP *et al.*, 1983; Ó FOIGHIL, 1986; Ó Foighil & Eernisse, unpublished data). Resolution of these relationships will require a multidisciplinary approach, applied to a variety of populations of this near-cosmopolitan genus.

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LITERATURE CITED

AFZELIUS, B. A. 1972. Sperm morphology and fertilization biology. Pp. 131–143. *In:* R. A. Beatty & S. Gluecksohn-Waelsch (eds.), Proceedings of the international symposium on the genetics of the spermatozoon. Edinburgh University Genetics Department.

BALLANTINE, D. & J. E. MORTON. 1956. Filtering, feeding and digestion in the lamellibranch *Lasaea rubra*. Jour. Mar. Biol. Assoc. U.K. 35:241–274.

BARNARD, K. H. 1964. Contributions to the knowledge of South African marine Mollusca. Pt. 5. Lamellibranchiata. Ann. S. Afr. Mus. 47:361–593.

BEAUCHAMP, K. A. 1985. The reproductive ecology of a brooding, hermaphroditic clam, *Lasaea subviridis*. M.Sc. Thesis, University of California, Santa Cruz. 59 pp.

BEAUCHAMP, K. A. 1986. Reproductive ecology of the brooding, hermaphroditic clam, *Lasaea subviridis*. Mar. Biol. 93:225–235.

BELL, G. 1982. The masterpiece of nature. Croom Helm: London. 635 pp.

BERGER, E. M. 1983. Population genetics of marine gastropods and bivalves. Pp. 563–598. *In:* W. D. Russell-Hunter (ed.), The Mollusca. Vol. 6. Academic Press: New York.

BLACKNELL, W. M. & A. D. ANSELL. 1974. The direct development of the bivalve *Thyasira gouldi* (Philippi). Thalassia Jugosl. 10:23–43.

BOOTH, J. D. 1979. Common bivalve larvae from New Zealand: Leptonacea. N.Z. Jour. Mar. Freshwater Res. 13:241–254.

BUCKLIN, A., D. HEDGECOCK & C. HAND. 1984. Genetic evidence of self-fertilization in the sea anemone *Epiactis prolifera*. Mar. Biol. 84:175–182.

BULL, J. J. & E. L. CHARNOV. 1985. On irreversible evolution. Evolution 39:1149–1155.

CARRIKER, M. R. & R. E. PALMER. 1979. Ultrastructural morphogenesis of prodissoconch and early dissoconch valves of the oyster *Crassostrea virginica*. Proc. Natl. Shellfish. Assoc. 69:103–128.

CHANLEY, P. & M. H. CHANLEY. 1970. Larval development of the commensal clam *Montacuta percompressa* Dall. Proc. Malacol. Soc. Lond. 39:59–67.

CHARLESWORTH, D. & B. CHARLESWORTH. 1981. Allocation of resources to male and female functions in hermaphrodites. Biol. Jour. Linn. Soc. 15:57–74.

CHARNOV, E. L. 1982. The theory of sex allocation. Princeton University Press: Princeton. 355 pp.

CHAVAN, A. 1969. Leptonacea Gray 1847. Pp. 518–537. *In:* R. C. Moore (ed.), Treatise on invertebrate paleontology. Pt. N. Mollusca (2). Geological Society of America and University of Kansas Press: Lawrence.

COE, W. R. 1931. Spermatogenesis in the California oyster, *Ostrea lurida*. Biol. Bull. 61:309–315.

CRISP, D. J., A. BURFITT, K. RODRIGUES & M. D. BUDD. 1983. *Lasaea rubra*: an apomictic bivalve. Mar. Biol. Lett. 4:281–294.

DALL, W. H. 1900. Trans. Wagner Free Inst. Sci. 3(5):1163.

DAUTZENBERG, P. 1929. Mollusca II. P. 378. *In:* A. Gruvel (ed.), Faune des Colonies Francaises. Vol. 3. Société d'Éditions Géographiques, Maritimes et Coloniales.

DAVENPORT, J. & J. B. BEARD. 1988. Observations on the temperature and salinity relations of *L. rubra*. Jour. Mar. Biol. Assoc. U.K. 68:15–23.

DELL, R. K. 1964. Antarctic and Subantarctic Mollusca: Amphineura, Scaphopoda and Bivalvia. Discovery Rept. 33:93–250.

FINLAY, H. J. 1928. The recent Mollusca of the Chatham Islands. Trans. N.Z. Inst. 59:232–286.

FISCHER, E. A. 1981. Sexual allocation in a simultaneously hermaphroditic coral reef fish. Amer. Natur. 117:64–82.

GAGE, J. D. 1979. Mode of life and behaviour of *Montacuta phascolionis*, a bivalve commensal with the sipunculan *Phascolion strombi*. Jour. Mar. Biol. Assoc. U.K. 59:635–657.

GLYNN, P. W. 1965. Community composition, structure and interrelationships in the marine intertidal *Endocladia muricata-Balanus glandula* association in Monterey Bay, California. Beaufortia 148:1–198.

GUSTAFSON, R. G., D. Ó FOIGHIL & R. G. B. REID. 1986. Early ontogeny of the septibranch *Cardiomya pectinata* (Carpenter, 1865). Jour. Mar. Biol. Assoc. U.K. 66:943–950.

HADERLIE, E. C. & D. P. ABBOTT. 1980. Bivalvia: the clams and their allies. Pp. 355–411. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford University Press, Stanford.

HEATH, D. J. 1979. Brooding and the evolution of hermaphroditism. Jour. Theor. Biol. 81:151–155.

JABLONSKI, D. & R. A. LUTZ. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. Biol. Rev. 58:21–89.

JACQUARD, A. 1975. Inbreeding: one word, several meanings. Theoret. Popul. Biol. 7:338–363.

JAENIKE, J. 1978. An hypothesis to account for the maintenance of sex within populations. Evol. Theory 3:191–194.

KAY, E. A. 1979. Hawaiian marine shells. Bernice P. Bishop Museum Press: Honolulu. 620 pp.

KEEN, A. M. 1938. New pelecypod species of the genera *Lasaea* and *Crassinella*. Proc. Malacol. Soc. Lond. 23:18–32.

LAMY, M. E. 1906. Liste des Lamellibranches recueillis par M. L. G. Seurat aux Iles Tuamotu et Gambier (1902–1905). Bull. Mus. Natl. d'Hist. Natur. 12:214.

LANDE, R. & D. W. SCHEMSKE. 1985. The evolution of self-fertilization and inbreeding. I. Genetic models. Evolution 39: 24–40.

MAYNARD SMITH, J. 1978. The evolution of sex. Cambridge University Press: Cambridge, U.K. 222 pp.

MCGRATH, D. & D. Ó FOIGHIL. 1986. Population dynamics and reproduction of hermaphroditic *Lasaea rubra*. Ophelia 25:209–219.

MORTON, J. E. 1954. The crevice faunas of the upper intertidal zone at Wembury. Jour. Mar. Biol. Assoc. U.K. 39:5–26.

MORTON, J. E. 1960. The responses and orientation of the bivalve *Lasaea rubra* (Montagu). Jour. Mar. Biol. Assoc. U.K. 36:383–405.

MORTON, J. E., A. D. BONEY & E. D. S. CORNER. 1957. The adaptations of *Lasaea rubra* (Montagu), a small intertidal lamellibranch. Jour. Mar. Biol. Assoc. U.K., 36:383–405.

OCKELMANN, K. W. 1965. Develomental types in marine bivalves and their distribution along the Atlantic coast of Europe. Pp. 25–35. *In:* L. R. Cox & J. F. Peake (eds.), Proceedings of the first European malacological congress. Conchological Society of Great Britain and Ireland, and Malacological Society of London.

OCKELMANN, K. W. & K. MUUS. 1978. The biology, ecology and behaviour of the bivalve *Mysella bidentata*. Ophelia 2: 211–221.

Ó FOIGHIL, D. 1985a. Fine structure of *Lasaea subviridis* and *Mysella tumida* sperm. (Bivalvia: Galeommatacea). Zoomorphology 105:125–135.

Ó FOIGHIL, D. 1985b. Sperm transfer and storage in the brooding bivalve *Mysella tumida*. Biol. Bull. 169:602–614.

Ó FOIGHIL, D. 1985c. Form, function, and origin of temporary dwarf males in *Pseudopythina rugifera* (Bivalvia: Galeommatacea). Veliger 27:72–80.

Ó FOIGHIL, D. 1986a. Reproductive modes and their consequences in three galeommatacean clams: *Mysella tumida, Pseudopythina rugifera* and *Lasaea subviridis* (Mollusca: Bivalvia). Ph.D. Thesis, University of Victoria. 256 pp.

Ó FOIGHIL, D. 1986b. Prodissoconch morphology is environmentally modified in the brooding bivalve *Lasaea subviridis* Mar. Biol. 92:517–524.

Ó FOIGHIL, D. 1987. Cytological evidence for self-fertilization in the brooding bivalve *Lasaea subviridis*. Int. Jour. Invert. Reprod. Dev. 12:83–90.

Ó FOIGHIL, D. & D. J. EERNISSE. 1987. Phosphoglucomutase allozyme evidence for an outcrossing reproductive mode in the hermaphroditic, brooding bivalve *Mysella tumida*. Jour. Moll. Stud. 53:223–228.

Ó FOIGHIL, D. & D. J. EERNISSE. In press. Geographically widespread, non-hybridizing, sympatric strains of the hermaphroditic, brooding clam *Lasaea* in the northeastern Pacific Ocean. Biol. Bull.

Ó FOIGHIL, D. & A. GIBSON. 1984. The morphology, reproduction and ecology of the commensal bivalve *Scintillona bellerophon* spec. nov. (Galeommatacea). Veliger 27:72–80.

OLDFIELD, E. 1961. The functional morphology of *Kellia suborbicularis* (Montagu), *Montacuta ferruginosa* (Montagu) and *M. substriata* (Montagu) (Mollusca; Lamellibranchiata). Proc. Malacol. Soc. Lond. 34:255–295.

OLDFIELD, E. 1964. The reproduction and development of some

members of the Erycinidae and Montacutidae (Mollusca, Eulamellibranchiata). Proc. Malacol. Soc. Lond. 36:79–120.

PONDER, W. F. 1971. Some New Zealand and subantartic bivalves of the Cyamiacea and Leptonacea with descriptions of new taxa. Rec. Dom. Mus. N.Z. 7:119–141.

ROBERTS, D. 1984. A comparative study of *Lasaea australis, Vulsella spongarium, Pinna bicolor* and *Donacilla cuneata* (Mollusca: Bivalvia) from Princess Royal Harbor, Western Australia. Jour. Moll. Stud. 59:129–136.

ROSEWATER, J. 1975. An annotated list of the marine mollusks of Ascension Island, South Atlantic Ocean. Smithsonian Contrib. Zool. 189:41 pp.

SEED, R. & R. J. O'CONNOR. 1980. Shell shape and seasonal changes in population structure in *Lasaea rubra* (Bivalvia: Erycinidae). Jour. Moll. Stud. 46:66–73.

SELANDER, R. K. 1970. Behaviour and genetic variation in natural populations. Amer. Zool. 10:53–66.

SELANDER, R. K. & D. W. KAUFMAN. 1973. Self-fertilization and genetic population structure in a colonizing land snail. Proc. Natl. Acad. Sci. U.S. 70:1186–1190.

SOOT-RYEN, T. 1960. Pelecypods from Tristan da Cunha. Res. Nor. Sci. Exped. Tristan da Cunha 49:1–47.

STRATHMANN, R. R. 1978. The evolution and loss of feeding larval stages of marine invertebrates. Evolution 32:894–906.

STRATHMANN, R. R. 1985. Feeding and non-feeding larval development and life history evolution in marine invertebrates. Ann. Rev. Ecol. Syst. 16:339–361.

STRATHMANN, R. R., M. F. STRATHMANN & R. H. EMPSON. 1984. Does brood capacity link adult size, brooding, and simultaneous hermaphroditism? A test with the starfish *Asterina phylactica*. Amer. Natur. 123:796–818.

TOWNSLEY, P. M., R. A. RICKEY & P. C. TRUSSEL. 1965. The laboratory rearing of the shipworm *Bankia setacea* (Tyron). Proc. Natl. Shellfish. Assoc. 56:49–52.

TRACEY, M. L., K. NELSON, D. HEDGECOCK, R. A. SCHLESSER & M. L. PRESSICK. 1975. Biochemical genetics of lobsters: genetic variation and the structure of the American lobster (*Homarus americanus*) populations. Jour. Fish. Res. Bd. Canada 32:2091–2101.

TURNER, R. D. & Y. M. YAKOVLEV. 1983. Dwarf males in the Teredinidae (Bivalvia: Pholadacea). Science 219:1077–1078.

UYENOYAMA, M. K. 1986. Inbreeding and the cost of meiosis: the evolution of selfing in populations practicing biparental inbreeding. Evolution 40:388–408.

WALLER, T. R. 1981. Functional morphology and development of veliger larvae of the European oyster *Ostrea edulis* Linné. Smithsonian Contrib. Zool. 328:70 pp.

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Possible Ontogenetic Change in the Radula of *Conus patricius* of the Eastern Pacific

by

JAMES NYBAKKEN

Moss Landing Marine Laboratories, P.O. Box 450, Moss Landing, California 95039, U.S.A.

Abstract. The eastern Pacific *Conus patricius* is a distinctive cone that shows a possible ontogenetic change in the radula tooth morphology. Smaller specimens have a very small juvenile tooth which lacks the barb, blade, and serration of the adult. At this time, the change can be weakly correlated only with size or age of the species.

INTRODUCTION

The prosobranch gastropod radula is known to show a certain amount of morphological variability within a species (Bandel, 1974; Borkowski, 1975; Carriker, 1943; Cernohorsky, 1970; Howe, 1930; Merriman, 1967; Rosewater, 1970; Houbrick, 1978). This variability has been most often correlated with sex (Robertson, 1971; Maes, 1966; Arakawa, 1958, 1969), and virtually all studies have dealt with adult radulae. Until recently, no studies appear to have followed the ontogenetic development of the prosobranch radula between postmetamorphic juveniles and adults. Such ontogenetic change was recently reported for *Epitonium billeeana* by Page & Willan (1988) and for *Conus magus* by Nybakken & Perron (1988). In the case of *C. magus,* the change was correlated with diet, as the adult is a piscivore and the juveniles are too small to consume fish. In *E. billeeana,* a protandric hermaphrodite, the radula morphology changed when the individuals changed sex.

In the course of a comparative radula study of West American species of *Conus,* Nybakken (1970b) uncovered a difference in the radulae of what were believed to be adult and juvenile *Conus patricius* (Hinds, 1843). At that time, a paucity of specimens precluded a more extensive study of the radula of *C. patricius* to confirm or deny the original single observation. Since that time, additional specimens have become available, which now establish the possible occurrence of an ontogenetic change. It is the purpose of this paper to document this change and to suggest the reasons for its occurrence.

MATERIALS AND METHODS

Specimens of *Conus patricius* were obtained from the 1967 Pillsbury Expedition to the Gulf of Panama (Nybakken, 1971), the Los Angeles County Museum, the Academy of Natural Sciences of Philadelphia, and from the personal collection of Mr. Alex Kerstitch. From these collections, a total of nine specimens yielded radulae which could be analyzed. These specimens ranged in shell length from 27.1 to 83.5 mm. The geographical range was from the Sea of Cortez to the Gulf of Panama.

Each individual was measured with vernier calipers for total shell length and width at the widest part of the shell. The animal was then extracted and the radula sac dissected out. The radula sac was transferred to a depression slide, where the teeth were freed from the soft tissue by dissolving the latter in a 5.25% sodium hypochlorite solution. Freed radula teeth were washed in two rinses of water and mounted directly from water into polyvinyl lactophenol on glass slides. Radulae were examined under a compound microscope equipped with a differential interference contrast system after Nomarski. Drawings of the individual teeth were made using a drawing tube.

In addition to the above specimens, Dr. Alan Miller provided slides of the gut contents of two specimens of *Conus patricius* that had been taken in Panama. In this latter case, the specimens were not seen.

Descriptive terminology in the description of the radula tooth follows Nybakken (1970b) and Kohn *et al.* (1972).

RESULTS

Of the nine *Conus patricius* dissected, four were male, four female, and one could not be assigned to a sex. With one exception, all of the smaller individuals were female and all of the larger, male. The exception was an 83.5 mm female.

Two distinct types of radula teeth were observed (Figure 1). The juvenile tooth was found in four specimens in

which the shell length ranged from 27.1 to 53.4 mm. The adult tooth was found in five specimens that ranged in size from 59.9 to 83.5 mm. Both radula types included males and females.

The adult tooth (Figure 1A) is elongate and characterized by a structure in which the serration is long relative to the lengths of the barb and blade and terminates in a rounded cusp about halfway down the shaft. There is virtually no waist. Each tooth is surmounted at the distal end by a short, pointed barb on one side, opposed by a truncated, short blade on the other. The adult tooth is similar to those of *Conus fergusoni* and *C. princeps*.

The juvenile tooth (Figure 1B) is very different. It is proportionately much smaller in size, and there is no indication of barb, blade, or serration. The basal, or proximal, part of the shaft is thicker than the distal part. There is also a very large opening to the central lumen.

Feeding data for *Conus patricius* are very sparse. The only information available was contained in the two slides of gut contents from adult-sized cones that were received from Dr. Alan Miller. Both slides had polychaete setae on them. One had the setae of the family Aphroditidae, and the other had setae of the families Aphroditidae and Spionidae. The radula condition of these specimens is unknown. The adult radula of *C. patricius* is very similar to that of *C. princeps*, which consumes polychaetes (Nybakken, 1979), so it is not surprising that polychaete remains were also found in *C. patricius*.

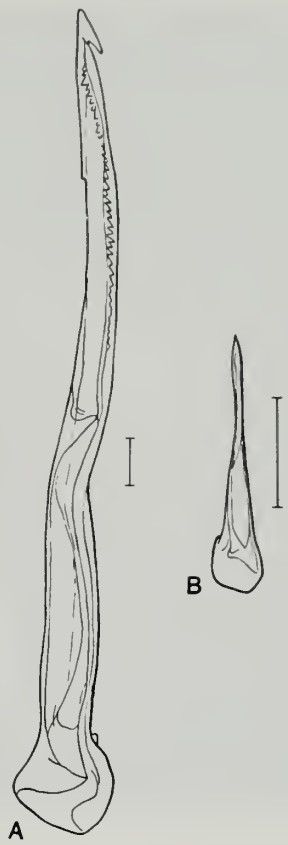

Figure 1

A. The radula of an adult *Conus patricius*. B. The radula of a juvenile *Conus patricius*. The length of the scale bar is 0.1 mm for both figures.

DISCUSSION

Although the number of individuals is small ($n = 9$), a number of factors strongly suggest that there is a decided ontogenetic change that occurs in the radula of *Conus patricius*. In the first place, *C. patricius* is a very distinctive cone. The characteristic pyriform shape is found in both the juveniles and adults and in no other eastern Pacific congeners (Figure 2). Therefore, it appears that we are not dealing with two species, one small and one large. This is reinforced by the finding of two similar-sized individuals, one 53.4 mm long and the other 59.9 mm long. The 53.4 mm individual, a male, possessed the juvenile radula and the 59.9 mm individual, also a male, the adult radula (Figure 2). Both individuals were collected in the same locality at the same time.

This case of two specimens of almost the same size having different radulae also suggests that the radula change, when it occurs, must be rapid. This is supported by the finding, in *Conus magus*, that an intermediate radula tooth type occurred only in specimens within a 3-mm size range (Nybakken & Perron, 1988).

The change in radula is not due to sex, since among the nine specimens, adult and juvenile radulae were found in both females and males.

The juvenile tooth of *Conus patricius* is almost identical to the juvenile radula tooth of *C. magus* (Nybakken & Perron, 1988). However, as an adult, *C. magus* is a piscivore; whereas, from our limited evidence here, we presume *C. patricius* as an adult is a vermivore. Similarity in morphology between the juvenile teeth of species in which adult teeth and diet are very different suggests that both juveniles could have similar diets, but this contention cannot now be answered because of lack of dietary information for juvenile *C. patricius*. Nybakken & Perron (1988) have, however, demonstrated that juveniles of *C. magus* consume polychaetes of the family Syllidae. If tooth morphology is correlated with diet in this case, as it is in some *Conus* (Lim, 1969; Nybakken, 1970a), it could be that the juveniles of these much larger cones are also eating syllids or other small polychaetes.

While I have established that there is a change in tooth structure in *Conus patricius*, I cannot correlate it with diet and can only very weakly correlate it with size or age. Nor can I demonstrate how the change might come about. I can, however, offer some speculation. Marsh (1977) demonstrated that, in the radula development of the adults of several species of *Conus*, each tooth is formed initially by odontoblasts and then finished and hardened by a tissue called the superior epithelium. It is therefore possible that

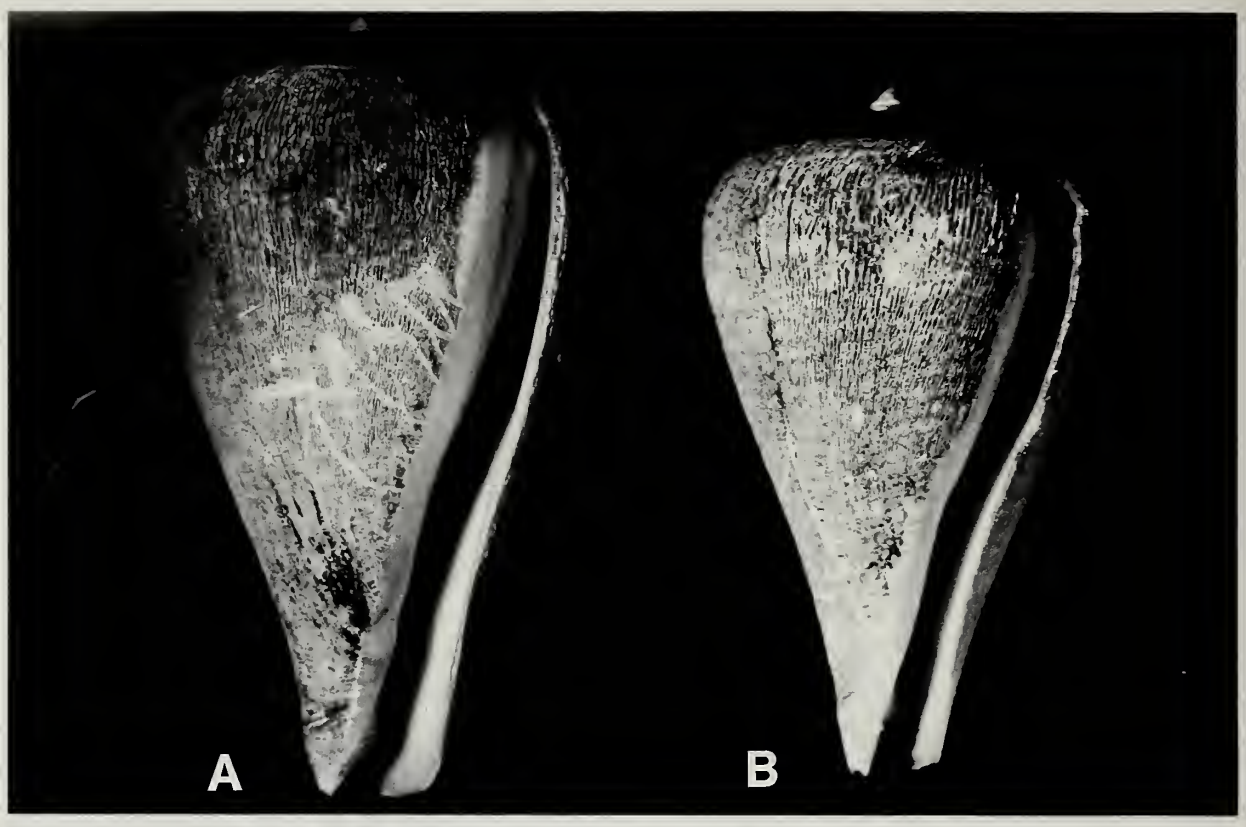

Figure 2

A. A specimen of *Conus patricius,* 59.9 mm in shell length, which contained an adult radula. B. A specimen of *Conus patricius,* 53.4 mm in shell length, which contained a juvenile radula.

in juvenile *C. patricius,* and perhaps other *Conus* as well, only the odontoblasts are first active, and they secrete the initial or juvenile tooth. Then later, when the animal is larger and ready to change diet, the superior epithelium is activated and the adult tooth is formed.

LITERATURE CITED

Arakawa, K. Y. 1958. On the remarkable sexual dimorphism of the radula of *Drupella*. Venus 19:206–214.

Arakawa, K. Y. 1969. On some problems of sexually dimorphic radulae. Venus 28:125.

Bandel, K. 1974. Studies on the Littorinidae from the Atlantic. Veliger 17(2):92–114.

Borkowski, T. V. 1975. Variability among Caribbean Littorinidae. Veliger 17(4):369–377.

Carriker, M. R. 1943. Variability, developmental changes and denticle replacement in the radula of *Lymnaea stagnalis appressa* Say. Nautilus 57(2):52–59.

Cernohorsky, W. O. 1970. Systematics of the families Mitridae and Volutomitridae (Mollusca: Gastropoda). Bull. Auckland Institute and Museum No. 8:iv + 190 pp., 18 pls.

Houbrick, R. S. 1978. The family Cerithiidae in the Indo-Pacific. Part I. The genera *Rhinoclavis, Pseudoverlagus,* and *Clavocerithium*. Monogr. Mar. Mollusca 1:1–130.

Howe, S. W. 1930. A study of the variations in the radula of a snail with particular reference to the size of the median teeth. Nautilus 44(2):53–56.

Kohn, A. J., J. Nybakken & J. J. Van Mol. 1972. Radula tooth structure of the gastropod *Conus imperialis* elucidated by scanning electron microscopy. Science 176:49–51.

Lim, C. F. 1969. Identification of the feeding types in the genus *Conus* Linnaeus. Veliger 12(2):160–164.

Maes, V. O. 1966. Sexual dimorphism in the radula of the muricid genus *Nassa*. Nautilus 79:73–80.

Marsh, H. 1977. The radular apparatus of *Conus*. Jour. Moll. Stud. 43:1–11.

Merriman, J. A. 1967. Systematic implications of radular structures of West Coast species of *Tegula*. Veliger 9(4):399–403.

Nybakken, J. 1970a. Correlation of radula tooth structure and food habits in three vermivorous species of *Conus*. Veliger 12(3):316–318.

Nybakken, J. 1970b. Radular anatomy and systematics of the west American Conidae (Mollusca, Gastropoda). Amer. Mus. Novitates No. 2414:29 pp.

Nybakken, J. 1971. The Conidae of the Pillsbury Expedition to the Gulf of Panama. Bull. Mar. Sci. 21(1):93–110.

Nybakken, J. 1979. Population characteristics and food resource utilization of *Conus* in the Sea of Cortez and west Mexico. Jour. Moll. Stud. 45:82–97.

NYBAKKEN, J. & F. E. PERRON. 1988. Ontogenetic change in the radula of *Conus magus*. Mar. Biol. 98:239–242.

PAGE, A. J. & R. C. WILLAN. 1988. Ontogenetic change in the radula of the gastropod *Epitonium billeeana* (Prosobranchia: Epitoniidae). Veliger 30(3):222–229.

ROBERTSON, R. 1971. Sexually dimorphic archaeogastropods and radulae. Ann. Rept. Amer. Malacol. Union for 1970: 75–78.

ROSEWATER, J. 1970. The family Littorinidae in the Indo-Pacific. Part 1. The subfamily Littorninae. Indo-Pacific Mollusca 2(11):417–479.

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The Radula and Penial Style of *Alderia modesta* (Lovén, 1844) (Opisthobranchia: Ascoglossa) from Populations in North America and Europe

by

J. SHERMAN BLEAKNEY

Biology Department, Acadia University, Wolfville, Nova Scotia, Canada B0P 1X0

Abstract. Radulae and penial styles of *Alderia modesta* (Opisthobranchia: Ascoglossa), collected in Europe and on Pacific and Atlantic coasts of North America, were examined using light and scanning electron microscopes. There was no evident endemism in spite of geographic distances. Teeth from 81 specimens were counted and measured, and revealed considerable variation within size classes. On an individual basis, total number of teeth varied from 17 to 43; number of teeth in the ascending limb from 3 to 7; number in the descending limb from 5 to 19; and number in the ascus from 1 to 32. Ultrastructural details revealed by SEM photographs of teeth and penial styles indicated the inadequacy of most diagrams available in the literature.

INTRODUCTION

The order Ascoglossa (=Sacoglossa) is an assemblage of about 200 species of opisthobranch mollusks which feed by piercing cell walls of marine algae or marine angiosperms and sucking out the cell sap (Jensen, 1980). Their radula consists of but a single row of teeth, and as new teeth are added to the radular ribbon, older teeth are discarded into a unique storage sac, the ascus. Jensen (1980) reviewed literature pertaining to the ascoglossan feeding apparatus and the various prey species categories. She noted that there are structural differences in radular teeth between genera and species, but that usually the examination of only one radula per species formed the basis for this information.

Each radula consists of an ascending row (dorsal limb) of teeth, a descending row (ventral limb) capped by the current single protruding piercing tooth (this is not a rasping radula), and an ascus sac which contains all previously produced teeth. There is, then, considerable potential for numerical variation within these three sub-units of the radula. Analysis of 230 radulae of *Elysia chlorotica* Gould, 1870 (Raymond & Bleakney, 1987) demonstrated surprising numerical variation and revealed just how inadequate was the available information (summarized for that species in table 3 of Jensen, 1980).

Alderia modesta (Lovén, 1844) is an unusual ascoglossan in that it is limited to tidal marshes and estuarine flats, is consequently amphibious, and is commonly found "basking in the sun" upon *Vaucheria* algal mats, its principal food, at substrate surface temperatures of 25.5°C (Bleakney & Meyer, 1979). This sea slug exhibits nil variation in gross anatomy in spite of its exceptional latitudinal and longitudinal distribution: northern Norway to the Mediterranean, western Greenland to New Jersey, and British Columbia to California.

The purpose of this present study was to investigate geographic variation in the radula and penial style (the hypodermic insemination apparatus) of *Alderia modesta.* Radulae and penial styles from diverse geographic areas were examined by means of light microscopy and then examined further with a JEOL JSM-255 scanning electron microscope. However, in order to discuss variation in the fine anatomy of these two organs, the illustrations presently available in the literature must be modified somewhat. A, B and C of Figure 1 depict attempts by three different authors to represent one radular tooth. Only the drawings by Evans (1953) convey the basic anatomy, but only an SEM could provide the ultrastructural detail (Figures 1D–G) needed for the present comparative study. In Figure 2, the three-dimensional twist configuration of the tip of the spine of the penetrant style (Figure 2C) and the imbricated scales along the inner curvature (Figures 2D, E), were only revealed through SEM techniques.

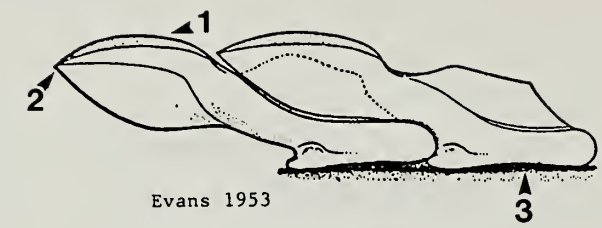
MATERIALS AND METHODS

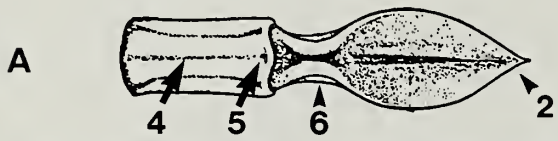
With the exception of the Danish specimens supplied by Dr. Kathe R. Jensen, all specimens were collected by the

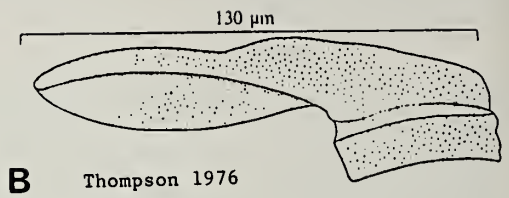
Table 1

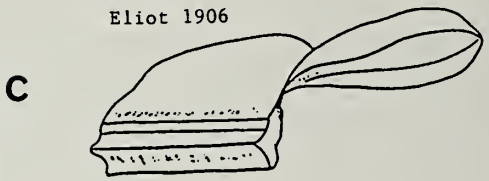
Numbers of radular teeth in *Alderia modesta* relative to body length, from seven different geographic regions. BC = British Columbia; W = Washington; NS = Nova Scotia; NF = Newfoundland; P = Pool Hrb., England; N = Norfolk, England; D = Denmark. Radular teeth lost during preparation procedures are designated *. The symbol / in the ascus columns indicates that the descending tooth row continued uninterrupted into the ascus as a coil.

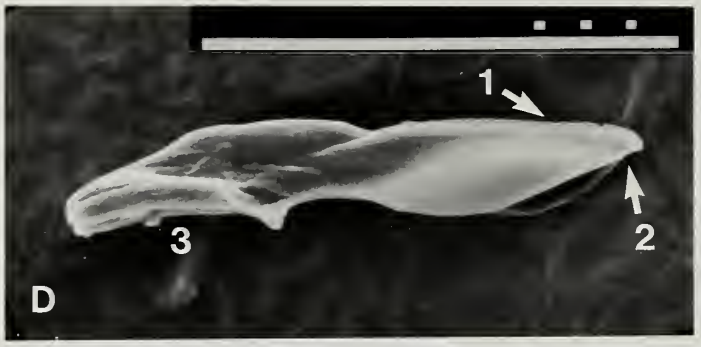
Body length (mm)	Ascending tooth row							Descending tooth row							Teeth in ascus							Tooth total						
	BC	W	NS	NF	P	N	D	BC	W	NS	NF	P	N	D	BC	W	NS	NF	P	N	D	BC	W	NS	NF	P	N	D
12			4							7							15							26				
(n = 2)			4							10							14							28				
10			4							9							10							23				
(n = 2)			5							11							9							25				
9							6							9							21							36
(n = 2)							4							15							3							22
8			5							16							/							21				
(n = 2)			5							19							/							24				
		5	5				5		7	7				10		11	15				9		23	27				24
7		4	5				4		6	8				12		*	14				3		*	22				19
(n = 10)		4	5						9	6						12	11						25	22				
			6							5							27							38				
			5							18														23				
	4	5	4				4	7	9	7				12	*	9	10				4	*	23	21				20
	5							7							*							*						
6	5							6							32							43						
(n = 9)	5							6							16							27						
	4							6							14							24						
	5							6							16							27						
	4	4	5	5	4		4	6	9	6	5	7		12	10	8	*	25	7		1	20	21	*	35	18		17
	5	4	4	4	6		5	5	15	6	6	7		12	16	/	17	22	12		3	23	19	27	32	25		20
5	6	4	5	5	5			7	7	15	6	6			22	13	/	29	13			35	24	20	40	24		
(n = 21)			4		5					15		7					/		8					19		20		
					4							7							9							20		
					5							6							10							21		
	4	4	4	4	5	5		7	16	15	6	7	5		26	/	/	20	10	27		37	20	19	30	22	37	
4	5	5	4	4	4	5		6	14	15	7	8	6		14	/	/	10	7	24		25	19	19	21	19	35	
(n = 20)	4	5	5	4		6		6	7	6	11		7		10	7	*	6		18		20	19	*	21	19	35	
				3		5					8		9					10		20					21		34	
						4							5							27							36	
			4	4	4	6				14	5	15	6				/	21	14	24				18	30	33	36	
3			4	4	5	5				14	6	6	7				/	14	14	22				18	24	25	34	
(n = 13)			4	4		4				14	5		5				/	12		30				18	21		39	
						7							7							24							38	
						5							6							23							34	
Total n = 81			Range: 3-7							Range: 5-19							Range: 1-32							Range: 17-43				


1
2
3
Evans 1953


A
4
5
6
2


130 µm
B
Thompson 1976


Eliot 1906
C


1
2
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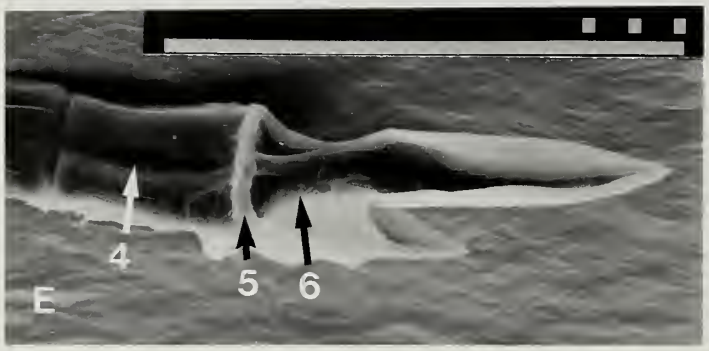
D


4
5
6
E

3
F

2
1
G

author. The localities, collecting dates, and the number of specimens from those samples utilized for radular tooth counts were (from west to east): (1) British Columbia, Vancouver Island, Bamfield Marine Station, August 1980 (n = 12); (2) Washington State, San Juan Island, Friday Harbour Laboratories, September 1980 (n = 10); (3) Nova Scotia, Minas Basin, 1966, 1969, 1975, 1976, 1982, 1985 (n = 22); (4) Newfoundland, Parsons Pond (northwest coast), August 1985 (n = 10); (5) England, Pool Harbour, June 1979 (n = 10); (6) England, Norfolk, Burnan Deepdale, June 1980 (n = 10); and (7) Denmark, Resund, Averre Beach, October 1964 (n = 7).

Although body length of *Alderia modesta* ranged from 3 to 12 mm, only 8 specimens exceeded 7 mm. Table 1 is a compilation of body length, geographic origin, and numbers of teeth in ascending limb, descending limb, ascus, and total.

In addition to the above 81 specimens, others were examined, photomicrographs taken, and still others were dissected for their radulae and penial styles and these were mounted for SEM examination. The techniques employed were described previously in Bleakney (1982) and in Raymond & Bleakney (1987) and involve dissociation of tissues by Beckman Tissue Solubilizer #450 (BTS-450). SEM mounts were made of radulae from British Columbia (n = 4), Nova Scotia (n = 2), Newfoundland (n = 1), and England (n = 3). Penial styles were prepared for SEM from all sites except Norfolk: British Columbia (n = 3), Washington (n = 5), Nova Scotia (n = 5), Newfoundland (n = 2), England (n = 1), and Denmark (n = 2).

Also recorded was the length of the base and the cusp of the single feeding tooth in each radula, in hopes of finding regional differences in that ratio.

To illustrate ontogenetic changes in tooth shape, and to record the one minor geographic variation noticed, each tooth in an entire radular series was measured for a specimen from Washington and from Denmark and these data are summarized in Table 2 and Figure 9.

RESULTS

There was remarkably little variation from population to population and certainly no indication of geographic differences that warrant taxonomic consideration, in this writer's opinion. The highest ascus tooth counts fell to Newfoundland and Norfolk, as much as double that of other areas. In the various categories of tooth counts, and for incidence of coiled radular ribbon, the Washington sample was similar to Nova Scotia, not adjacent British Columbia. Admittedly, the sample sizes were small, but columns of figures in Table 1 are encouragingly consistent within each sample.

Numbers of Teeth

Considering the entire sample of 81 radulae, it is evident that for *Alderia modesta*:

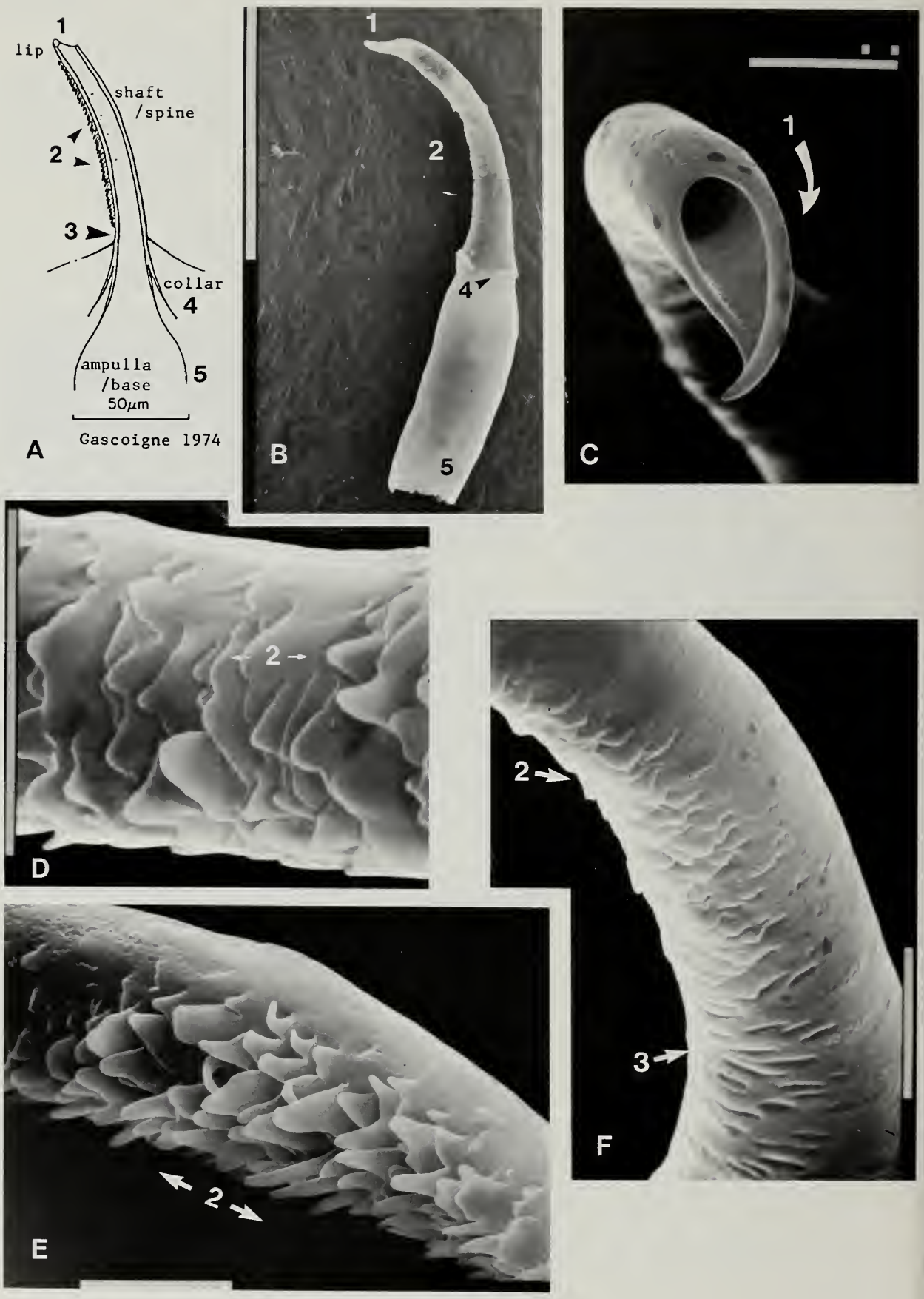
(1) The number of ascending teeth rarely deviates from 4 or 5, with a range of 3 to 7.
(2) The number of descending teeth is more difficult to delimit because the older teeth may quickly separate from the ribbon and form a jumble in the ascus or they may remain attached for a longer period and form an extended row (Figure 3), or may never detach and thus form a continuous coil, housed in the ascus (Figure 4). Only Washington and Nova Scotia samples had individuals with completely coiled tooth complements. The usual number of descending teeth is 6 or 7, but does range from 5 to 19. Series of 9 or more connected descending teeth were common in samples from Washington (6 of 10), Nova Scotia (13 of 21), and Denmark (7 of 7). Only the British Columbia sample lacked the long coiled radula.
(3) The number of loose teeth packed in the ascus sac varied from 1 to 32, and reflected the degree of persistence of the radular ribbon with attached teeth. There is considerable individual variation evident, but at the regional level the highest counts were British Columbia (32), Norfolk (30), and Newfoundland (29). However, the highest counts relative to other samples in the same size classes were the 3-mm class from Norfolk and the 5-mm class from Newfoundland, which were often double the number of teeth (Table 1).
(4) The highest individual total number of teeth was 43 from British Columbia, but Norfolk had the most individuals with totals exceeding 30 teeth. The range for the 81 specimens was 17 to 43.

When comparisons were made between size classes from the same locality, there was often little relationship between body length and total number of teeth. Nova Scotia

←

Figure 1

A–C. Diagrams of radular teeth of *Alderia modesta* reproduced from the literature (A, from Evans, 1953; B, from Thompson, 1976; C, from Eliot, 1906) with comparative SEM micrographs (D–G) indicating six features of these diagrams which are inaccurate: (1) there is a narrow dorsal keel on the cusp; (2) there is a slightly hooked but blunt tip on the cusp; (3) the tooth base, from lateral aspect, is definitely concave; (4) the tooth base has a deep ventral trough; (5) the tooth base is bordered anteriorly by a prominent transverse ridge; (6) the base of the cusp, ventral aspect, has 3 not 2 ridges. D is from Newfoundland; E is ventral aspect of spatulate tooth, base and cusp from Norfolk, England; F is entire radula with ascus, body length 4 mm, Norfolk; G is cusp portion of two teeth, dorsal and ventrolateral aspects, from Nova Scotia. Bar scales of D, E, and F equal 100 μm, and the scale in G is 10 μm.


1
lip
shaft
/spine
2
3
collar
4
ampulla
/base
5
50μm
Gascoigne 1974
A
1
2
4
5
B
1
C
2
D
2
3
F
2
E

animals of 5 mm can have tooth counts equal to 12-mm specimens. Comparing different localities is even more striking. For example, some 3-mm Norfolk specimens have double the tooth count of 3-mm Nova Scotia specimens, and have as much as 1.5 times the number of teeth as the 12-mm Nova Scotia size classes (Table 1).

Shape and Size of Teeth

The individual teeth of *Alderia modesta* are essentially identical throughout the species' range. There are four preliminary teeth; the first is nearly triangular, the second is rectangular, the third has a rectangular base with a short spike, and the fourth is the first tooth to possess the long spatulate cusp (Figures 5–7). The cusp becomes relatively larger in the fifth and succeeding teeth. The ontogenetic change in base-cusp ratio is evident in Table 2 and Figure 9, and the two examples chosen represent the extremes observed in this study. Only the Danish specimens had these relatively larger tooth bases, and this was most pronounced in the youngest teeth. At the 8th tooth the base-cusp ratio of the two samples converges and continues in parallel (Figure 9) even though the Danish teeth are larger. The two specimens selected for Table 2 had the continuous coiled radular ribbon and thus all the teeth were in their original sequence. Each was measured although only every second tooth is listed in Table 2.

The base-cusp ratio of the single projecting feeding tooth (Figures 4, 5) in 70 specimens varied from 1.12 to 2.1, but this range had been reached at body lengths of only 4 and 5 mm. In fact, 11 specimens in the 4- to 6-mm size class had ratios of 1.9 to 2.1 which equalled or exceeded the base-cusp ratio of larger 10- to 12-mm size classes. All but 9 specimens were within ratios of 1.5 to 1.9, and no geographic differences were evident.

The length of the largest feeding tooth recorded from each locality is listed in Table 3 under body length classes. The size range of that same tooth within the 3-mm body length is also listed and serves to emphasize once again the surprising extent of individual variation and the equally surprising paucity of evident geographic races derived from the potential within that variation.

There is, however, one peculiar relationship evident in Table 3, and that is between tooth maximum and the year in which the specimens were collected. The largest teeth (over 200 μm) are from the 1960s, the smallest (near 135 μm) from 1979–1980, and the intermediates (at 157 μm) from 1985. In light of Raymond & Bleakney's (1987) discovery of annual fluctations in tooth production in *Elysia chlorotica*, the above "coincidence" regarding tooth size may have some validity.

Penial Style

Examination of penial style morphology by light microscopy indicated no differences from one population to another (Figure 8) and, therefore, geographic comparisons were not attempted. There were, however, size differences associated with increased body length which indicate that this structure, unlike the teeth, is either continually being restructured (length and diameter) or is periodically discarded and renewed. These data, with information from the literature, are summarized in Table 4.

Two ultrastructural features were examined with the SEM in hope of detecting geographic differences. The first was the curl of the penetrant tip of the style (Figure 2C). No variation was evident. Using light microscopy, Gascoigne (1974) reported this curled point as merely a thickened edge at one side of the orifice (Figure 2A).

The second feature examined was the scaly surface of the inner curvature of the spine and in this case a minor "variant" was noted in the longer scales of the Newfoundland samples (Figure 2E). This may or may not be a constant feature of west coast Newfoundland populations. Gascoigne (1974, 1976) understandably concluded these scales were spinules and first reported them as occurring in a narrow band (1974) and later (1976) as arranged in a single row. His diagram (reproduced here as Figure 2A) omitted much of the inflated basal cylinder (Figures 2B, 8). Not previously reported in the literature are the pits and slits at the base of the style spine (Figure 2F). These vary in size, shape and depth, but again individual variation negated any hope of discovery of a region exhibiting distinct endemism.

DISCUSSION

Jensen (1980: table 4) indicated that no information was then available on the numbers and size of *Alderia modesta* teeth, even though she cited Evans (1953) in which his fig. 2 has a tooth formula of 4/7 plus ascus, and a stated feeding tooth length of 135 μm. Evan's measurements agree well with the present study. Thompson (1976) reported tooth counts of 20 and 16 but did not indicate how many in the ascending and descending series. His specimen with 16 teeth was 3 mm long and had 9 worn teeth in the ascus, an unusually low ascus count (Table 1).

The basic anatomy of the buccal mass and of the radular

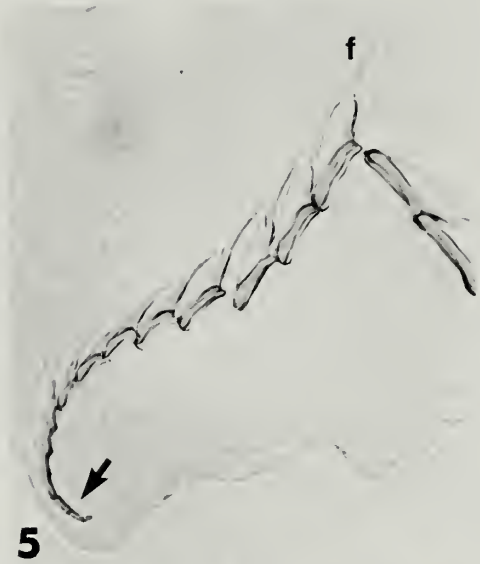
←

Figure 2

A. Diagram of penial style of *Alderia modesta* from Gascoigne (1974). B–G. SEM micrographs illustrating finer details: B is from Nova Scotia, note relative size of base; C is the penetrant tip of a 7-mm specimen, Nova Scotia; D is imbricated scales on inner curvature of spine, Nova Scotia; E is typical of Newfoundland samples; F is basal area of spine showing pits and grooves noted in all samples, this one from Washington. Scale bar in B represents 100 μm; in C–F, bar is 10 μm.

3

4



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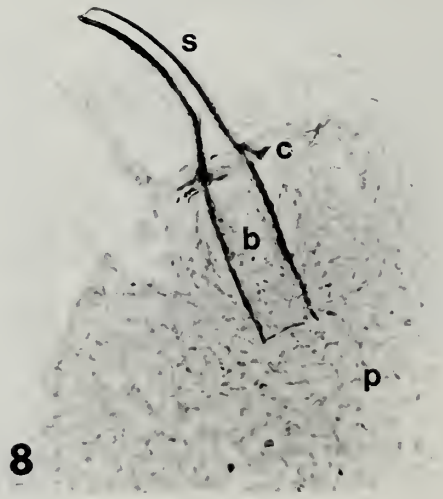

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Table 2

Base-cusp lengths in μ and their ratios, of a series of teeth from one Danish 7-mm specimen and from one 5-mm Washington State *Alderia modesta*. Each possessed 18 teeth and the 15th was the projecting feeding tooth. Of the seven populations sampled, only the Danish slugs had such large tooth bases.

Tooth no. in series	Denmark Tooth length				Washington State Tooth length			
	Base	Cusp	Total	B-C ratio	Base	Cusp	Total	B-C ratio
4	18.0	22.5	40.5	1.25	9.0	27.0	36.0	3.0
6	22.5	31.5	54.0	1.4	13.5	34.0	47.0	2.5
8	22.5	45.0	67.5	2.0	18.0	36.0	54.0	2.0
10	31.5	58.5	90.0	1.85	22.5	45.0	67.5	2.0
12	40.5	76.5	117.0	1.88	29.0	54.0	83.0	1.8
14	54.0	99.0	153.0	1.83	36.0	65.0	101.0	1.8
15f	63.0	99.0	162.0	1.57	36.0	67.5	103.5	1.9
16	63.0	103.5	166.5	1.64	45.0	72.0	117.0	1.6
18	76.5	121.5	198.0	1.58	45.0	79.0	124.0	1.75

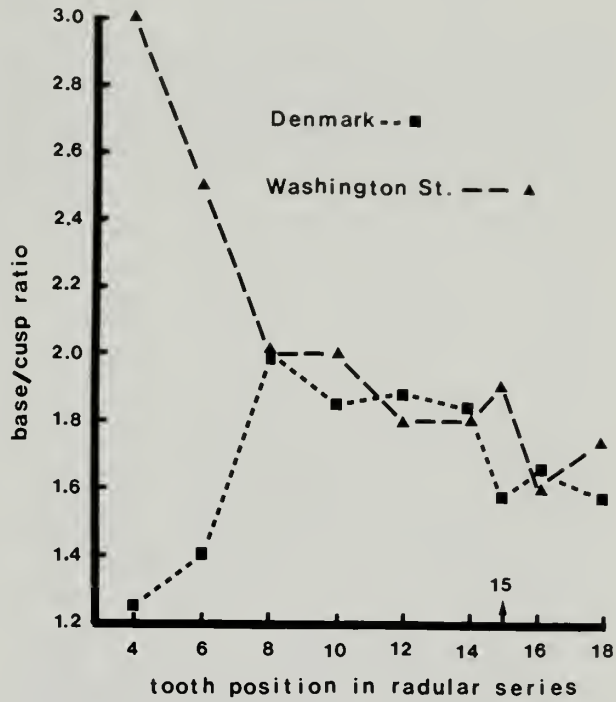

Figure 9

Plot of data in Table 2 showing the extreme initial difference in base-cusp ratio and the rapid convergence to a common pattern.

teeth (Figure 1A) depicted so well by EVANS (1953), lacks only the finer details that SEM photographs can provide. These SEM anatomical refinements are assembled in Figures 1D–G, with the Evans drawings, and are: (1) narrow dorsal keel on cusp; (2) slightly hooked, but blunt tip on cusp; (3) base of tooth, lateral aspect, has a concave curvature; (4) base of tooth, ventral aspect, has a deep central trough; (5) base of tooth, ventral aspect is bordered anteriorly by a prominent transverse ridge; and (6) base of cusp, ventral aspect, has 3 not 2 ridges.

In spite of isolation between Atlantic and Pacific populations by both immense distances and time periods, distinct endemism is not evident in these samples of *Alderia modesta*. Genetic continuity is an unlikely explanation, as the Central American continuity between Atlantic and Pacific oceans closed about 2.5 million years ago, and the potential trans-arctic marine connection has recently undergone successive glaciations. To postulate a recent contiguous series of low-salinity coastal marsh habitats, a requisite for the food alga (*Vaucheria*) of *Alderia* across the arctic from Greenland to Alaska is unnecessary if not unreasonable. In fact, this author would argue that the evidence is against recent gene flow even between Europe and eastern North America. Considering deciphered continental drift patterns, the North Atlantic basin at its inception (90–70 million years ago) undoubtedly was a single faunal unit. The gradual distancing of those eastern and western shores has effectively separated the gene pools of

←

Explanation of Figures 3 to 8

Figure 3. Buccal mass with radula from 9-mm specimen of *Alderia modesta*, Denmark. Asd indicates ascending (dorsal) row of radula, dsd is descending (ventral) row with 9 teeth attached to the radular ribbon, whereas all previously formed teeth have detached and are packed into the ascus sac (asc).

Figure 4. Radula of 12-mm *A. modesta* from Nova Scotia, showing continuous coil of radular ribbon with retention of teeth in their original production sequence. The projecting piercing feeding tooth is indicated at f.

Figure 5. Descending series of 15 radular teeth from 4-mm *A. modesta*, Nova Scotia. Note 12 teeth with thick bases and long cusps, and the 3 small preliminary teeth (at arrow) without cusps. Feeding tooth is at f.

Figure 6. The first 11 teeth of a 4-mm *A. modesta*, Nova Scotia, showing dramatic morphological transition from tooth no. 3 to tooth no. 4, and the rapid increase in the mass of each subsequent tooth.

Figure 7. Part of ascus contents of 12-mm *A. modesta*, Nova Scotia, with the first 5 teeth numbered. Note the characteristic short spur on tooth no. 3 in contrast with the long cusp on tooth no. 4.

Figure 8. Typical penial style of *A. modesta* showing spine (s) protruding from top of large penis (p) in which the style base (b) with collar (c) is embedded. From a Danish specimen 6 mm in length.

Table 3

Length in μm of longest feeding tooth recorded for *Alderia modesta* from each geographic locality and the body length of that specimen. In the 3-mm body-length column, the entire range of sizes of the feeding tooth is listed. Note that the largest teeth are from 1960s populations, the smallest from 1979 to 1980.

Locality	Body length (mm) 3	4	5	6	7	9	12	Collection year
B.C.	—	—	—	135	—	—	—	1980
Wash.	—	—	—	—	135	—	—	1980
NS	108–153	—	216	—	238.5	—	225	1966, 1969
Nfd.	103–144	—	157.5	—	—	—	—	1985
Pool	76–135	—	135	—	—	—	—	1979
Norf.	99	130.5	—	—	—	—	—	1980
Denm.	—	—	—	—	—	202.5	—	1964

the two coasts, and it is evident that there has been ample time for speciation within these amphiatlantic genera, for at present only 64% of West Atlantic nudibranch species are amphiatlantic, and more strikingly, only two ascoglossan species of the seven species reported from the North American coast north of Cape Hatteras, also occur in Europe (Franz, 1970). If there were a transatlantic genome pipeline for benthic opisthobranchs, then many additional European estuarine and open coast species should occur on our Canadian shores, especially the ubiquitous intertidal genus *Limapontia* (with 3 species) which so often occurs in company with *Alderia modesta* in Europe. While arguing for genetic ultra-conservatism in *Alderia,* it is worth noting that *Placida dendritica* (Alder & Hancock, 1843) and the marsh anemone *Nematostella vectensis* (Stephenson, 1935) have a similar European and east-west coast of North America distribution, with no indication of speciation.

The potential, however, for some manifestation of genetic drift, mutations, and natural selection pressures is certainly there, as this species has a short life-span of perhaps 2 to 6 months (Clark, 1975) and can lay an average of 1000 eggs/day during the warmer months, after maturing within 10 days of its post-veliger metamorphosis (Seelemann, 1967). Also, within the Ascoglossa, radulae and penial styles can and have evolved into a variety of morphs (Gascoigne & Sartory, 1974). The minor degree of individual variation noted within my samples of *Alderia modesta* (tooth size, total number of teeth, coiled radula, penial scales) was enough to encourage this investigator to imagine that one or two of these minor features might possibly occur as a distinct characteristic in perhaps even one of these isolated populations. Only examination of larger samples over a period of several years might eventually reveal the following: (1) in Denmark (and Baltic region?) the radular ribbon always coils into the ascus; (2) in Newfoundland (and Greenland?) the penial scales are always long; and (3) along the Norfolk coast (and North Sea?) the rate of tooth production is always twice that of other regions. With more data it may become possible to demonstrate that these minor regional differences in tooth and penial morphology have restricted genetic latitude, whereas, absolute size and numerical differences fluctuate easily with an assortment of environmental parameters.

Table 4

Comparative lengths of penial styles of *Alderia modesta* relative to body length, from this study and the literature.

Locality	Body length (mm)	Penial style length (μm) Base	Spine	Total	Source
Nova Scotia					
Newfoundland					
Nova Scotia	3	50	70	120	This study
California	4	75	100	175	This study
	5	89	100	189	This study
British Columbia	5.5*	—	—	180	Hand & Steinberg, 1955
Washington	6	88	108	196	This study
State	7	100	125	225	This study
England	—	—	100	—	Gascoigne, 1974
England	—	—	120	—	Gascoigne, 1974

* An average.

Perhaps the overall anatomical uniformity of *Alderia modesta* populations should not be surprising because it may be the only representative of the entire family Alderiidae (Jensen, 1983). The atrophied heart, the random hypodermic insemination, the unusual Xanthophyta food, the highly amphibious habits, and so on, bespeak an exceptional history of adaptations. Perhaps *A. modesta* is an ancient genus from the base of the stiligerid line, as Gascoigne suggested (1985), and has survived the competition of more recent ascoglossan groups through its unique specializations. Comparison of the genome of *Alderia* with that of its antithesis the genus *Elysia* (with perhaps over 60 species) would add a valuable dimension to the recent significant series of discussion papers on evolution and adaptation within the Ascoglossa: Gascoigne (1976, 1985), Clark & Busacca (1978), Jensen (1980), and Clark & DeFreese (1987).

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LITERATURE CITED

Bleakney, J. S. 1982. Preparation of radulae and penial styles for SEM using 0.5 N quaternary ammonium hydroxide. Veliger 24:279–280.

Bleakney, J. S. & K. B. Meyer. 1979. Observation on saltmarsh pools, Minas Basin Nova Scotia 1965–1977. Proc. Nova Scotia Inst. Sci. 29:353–371.

Clark, K. B. 1975. Nudibranch life cycles in the northwest Atlantic and their relationship to the ecology of fouling communities. Helgoländer wiss. Meeresunters 27:28–69.

Clark, K. B. & M. Busacca. 1978. Feeding specificity and chloroplast retention in four tropical ascoglossa with a discussion of the extent of chloroplast symbiosis and the evolution of the order. Jour. Moll. Stud. 44:272–282.

Clark, K. B. & D. DeFreese. 1987. Population ecology of Caribbean Ascoglossa (Mollusca: Opisthobranchia): a study of specialized algal herbivores. Amer. Malacol. Bull. 5(2): 259–280.

Eliot, C. 1906. Notes on some British nudibranchs. Jour. Mar. Biol. Assoc. 7(3):333–383.

Evans, T. J. 1953. The alimentary and vascular systems of *Alderia modesta* (Lovén) in relation to its ecology. Proc. Malacol. Soc. Lond. 29(6):249–258.

Franz, D. R. 1970. Zoogeography of northwest Atlantic opisthobranch molluscs. Mar. Biol. 7(2):171–180.

Gascoigne, T. 1974. A note on some sacoglossan penial styles (Gastropoda: Opisthobranchia). Zool. Jour. Linn. Soc. 55(1): 53–59.

Gascoigne, T. 1976. The reproductive systems and classification of the Stiligeridae (Opisthobranchia: Sacoglossa). Jour. Malacol. Soc. Austral. 3(3–4):157–172.

Gascoigne, T. 1985. A provisional classification of families of the order Ascoglossa (Gastropoda: Nudibranchiata). Jour. Moll. Stud. 51(1):8–22.

Gascoigne, T. & P. K. Sartory. 1974. The teeth of three bivalved gastropods and three other species of the order Sacoglossa. Proc. Malacol. Soc. Lond. 41:109–126.

Hand, C. & J. Steinberg. 1955. On the occurrence of the nudibranch *Alderia modesta* (Lovén, 1844) on the central California coast. Nautilus 69(1):22–28.

Jensen, K. R. 1980. A review of the sacoglossan diets, with comparative notes on radular and buccal anatomy. Malacol Rev. 13(1–2):55–77.

Jensen, K. R. 1983. Preliminary index of species of Ascoglossa. Opisthobranch Newsl. 15(3):9–16.

Raymond, B. G. & J. S. Bleakney. 1987. The radula and ascus of *Elysia chlorotica* Gould (Opisthobranchia: Ascoglossa). Veliger 29(3):245–250.

Seeleman, U. 1967. Rearing experiments on the amphibian slug *Alderia modesta*. Helgoländer wiss. Meeresunters 15: 128–134.

Thompson, T. E. 1976. Biology of opisthobranch molluscs. Vol. I. The Ray Society: London. 207 pp.

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Shell Microstructure and Color Changes in Stressed *Corbicula fluminea* (Bivalvia: Corbiculidae)

by

ROBERT S. PREZANT

Department of Biology, Indiana University of Pennsylvania,
Indiana, Pennsylvania 15705, U.S.A.

ANTONIETO TAN TIU

Harbor Branch Oceanographic Institution, Ft. Pierce, Florida 33450, U.S.A.

AND

KASHANE CHALERMWAT

Nelson Biological Labs, Rutgers University,
Piscataway, New Jersey 08856, U.S.A.

Abstract. Specimens of *Corbicula fluminea* from Mississippi show altered internal shell color and microstructure when maintained under stressful conditions. Clams under laboratory conditions that "threaten" life-sustaining functions, as well as field collections of moribund animals, show conversion of typically purple highlighted internal shell to pure white, and conversion of a surficial complex crossed-lamellar microstructure to a form reminiscent of complex crossed-acicular. These changes possibly result from a shift in metabolic activities away from energy expenditures normally allocated to shell production and towards life-sustaining functions. Alternatively, the modified shell can be a reflection of internal shell dissolution under similar conditions, although dissolution studies reveal a different form of shell erosion. Additionally, crossed-acicular microstructures, at least as they appear in exposed shell layers, could be an environmentally induced product and should not be construed as a product of "normal" biomineralization processes.

INTRODUCTION

The question of environmentally induced changes in corbiculid shell form and structure has become more than an esoteric exercise in taxonomy. The interest coincides with the rapid invasion of *Corbicula* throughout North America (McMahon, 1982; Counts, 1986) and the incessant debate over the number of species occurring in North America. Prashad (1929) and Sinclair & Isom (1963) discussed variability in shell characters in the genus *Corbicula,* but Morton (1986) and Britton & Morton (1979) claimed that taxonomists have not distinguished significant differences in shell form within the genus but rather have overemphasized "slight or moderate variability in conservative shell characteristics." During the First International *Corbicula* Symposium, Britton & Morton (1979) suggested that a single species occurred in North America. Hillis & Patton (1979) and, more recently, McLeod (1986) presented electrophoretic evidence for two species of North American *Corbicula* (*i.e., C. fluminea* (Müller) and inconclusively *C. fluminalis* (Müller): the so-called white and purple forms respectively). Hillis & Patton (1979) also presented morphometric differences in shell form between their electrophoretically separated forms. One form, with a deeply purple internal shell, also has more shell annuli than the "white" form. Prezant & Tan Tiu (1985) found few significant microstructural shell differences between the two color "forms" but did note a slight (ca. 0.15%) difference in total shell organics, with the purple form having slightly more. The previous study did not include an examination of shell recessed beneath the peripherally undertucked periostracum. When this in-

ternal edge was examined (PREZANT & TAN TIU, 1986) a unique shell microstructure (spiral crossed-lamellar) was found in a large number of white forms of *Corbicula* (*i.e.*, *C. fluminea*) but has yet to be found in the purple form.

Since populations of *Corbicula* are found in North American lotic and lentic habitats (BRITTON, 1982) in various substrata over many ecologic provinces (MCMAHON, 1982), the bivalve may be suspected of being morphologically plastic. This paper reports variations in intraspecific internal shell color and microstructure in "white" *Corbicula* (*i.e.*, *C. fluminea*) under stressful environmental conditions. We have found that internal shell microstructures of *C. fluminea* are variable and can reflect environmental or physiological conditions. We further suggest that a crossed-acicular microstructure, as it appears in exposed shell layers, is an environmentally induced modification of a crossed-lamellar microstructure and should not be construed as a specific calcified microstructure.

MATERIALS AND METHODS

Living specimens of *Corbicula fluminea* were collected from sand and gravel bars in Tallahala Creek, Perry County, and from sand deposits within eroded rock "pools" in Strong River at D'Lo, Simpson County, Mississippi, U.S.A. All clams collected were of HILLIS & PATTON's (1979) white form (based on dimensions, shell shape, and annulus counts) but most exhibited a purple highlighted shell internally (though not the homogeneous, deep purple pigmentation of the "purple" or dark form).

Live animals, for baseline analyses, were immediately shucked upon collection or upon return to the laboratory. Valves were prepared for scanning electron microscopy as follows. Valves were dehydrated in absolute ethanol for 5–9 days prior to critical point drying in a Denton DCP-1 critical point drying unit. Liquid carbon dioxide was used as a direct transfer agent. Some specimens were fractured prior to drying. All specimens were mounted on aluminum stubs using silver paint and coated with a thin layer of gold. Specimens were examined at the University of Southern Mississippi in an AMR 1000A scanning electron microscope (SEM) at an accelerating voltage of 30 kV.

Initial experiments involved manipulating temperature and "food" regime using aged tap water at ambient and warm temperatures. (Food is placed in quotation marks to reflect the difficulties in getting active growth [*i.e.*, comparable to field growth] in the laboratory. While easy to maintain in apparent good health and with slight growth, large size and weight gains over long periods have yet to be reported for laboratory populations of *Corbicula fluminea*; in fact minimal and even degrowth are more common.) Four separate 38-L aquaria, with gentle outside filtration (with removable activated charcoal filters), were used to each hold six small (L = 6–12 mm) (L = maximum anteroposterior shell length) *C. fluminea* collected from Tallahala Creek in September 1982. Test animals were held in the individual test aquaria at 23°C (ambient field temperature at time of collection) and two aquaria were gradually brought up to 31°C over a 4-day period. Individual aquaria were then held at 23°C without "food," 23°C with "food," 31°C without "food," and 31°C with "food." The feeding regime followed a 3-day cycle. A pure concentrate of liquified (well-blended) spinach leaves was added to the "fed" aquaria in doses of 25 mL every 3 days. Just prior to feeding, outside filtration packs in all aquaria were removed and not replaced for 24 h. Aquaria were held at 12:12 light:dark cycles using 40 W fluorescent tubes located 10 cm above the water surface. A sudden power surge brought the heated, "fed" aquarium to 37°C 3 weeks into the experiment and resulted in strong physiological stress of specimens in that tank within the next week's time. Clams in the afflicted tank were carefully monitored and removed immediately upon observation of death or impending death (*i.e.*, gaping and nonresponsive). Experiments in all aquaria were terminated 4 weeks after initiation and valves prepared for SEM studies as noted above.

24-Hour Adduction

To examine *Corbicula* shell for internal shell erosion that could have co-occurred with stress induced during the previous experiment, studies were conducted to induce internal shell dissolution as might occur during anaerobiosis (Table 1).

At 1045 h on 10 November 1984, 250 clams (L = 5–15 mm) were collected from the Strong River. At the time of collection, air temperature was 20°C, water temperature was 18°C, pH 5.85, and conductivity was 62 mhos/cm. The water in the Strong River at D'Lo was running faster and higher than usual because of recent rains. Ten clams were sacrificed at 1130 h as baseline specimens. All other specimens were clamped shut (forced adduction) in the field and returned to the lab (ambient temperature = 19°C) where 10 specimens were sampled every hour for the next 25 h (the 0530 h sampling was missed so the study ran an additional hour to allow for 24 samples plus baseline). At sampling, the specimens were shucked, valves were prepared for SEM, and soft parts were preserved in Hollande-Bouine's fixative for future analysis.

7-Day Adduction

Clams (L = 5–15 mm) were collected from the Strong River on 10 November 1984 and held overnight in the laboratory in Strong River water at 18°C in a recirculating 19-L aquarium. Ten clams were sampled as a baseline and 70 others were force adducted using clothes pins and suspended in the aquarium. Each day for the next 7 days 10 additional clams were sampled. Specimens were prepared for SEM and soft parts fixed in Holland-Bouine's fixative for future analysis.

To explore the possibility that during dissolution calcium carbonate is preferentially lost leaving a remnant

Table 1

Sizes (averages) and results of 24-h *Corbicula fluminea* shell dissolution study. Experiment begun on 10 November and ended on 11 November 1984. (SD = standard deviation; *n* = number of individuals from sample examined by scanning electron microscopy.) Microstructural conditions indicated are from various regions of internal shell as indicated by code (A = under periostracum; B = just dorsal to periostracum; C = dorsal to B and inclusive of pallial line; D = just dorsal to pallial line; E and F = just dorsal to D; G = at level of ventral edge of adductor scars; H = at level of dorsal edge of adductor scars/lower edge of retractor scars; I = umbonal region). Only significant changes are noted.

Time	Length ± SD (mm)	Heigth ± SD (mm)	*n*	Microstruture condition
1130	13.9 ± 2.45	11.5 ± 1.93	9	Baseline condition.
1230	11.7 ± 1.06	10.1 ± 0.26	3	
1330	11.9 ± 1.38	10.2 ± 1.32	3	
1430	11.3 ± 0.91	9.4 ± 1.07	3	A–B: scattered pits.
				C: irregular pits; some fragmentation.
				D–F: narrowed lamels of irregular width.
				G–H: perforate blocks.
1530	11.7 ± 0.38	9.9 ± 0.23	3	G–H: cross-acicular pattern.
				I: smooth, porous.
1630	10.4 ± 1.30	8.6 ± 1.28	3	A–B: porous, some lamels protrude.
				C–F: lath fragments present, rare.
1730	11.3 ± 0.76	9.6 ± 0.83	3	A–B: lath fragments.
				C: highly porous.
1830	10.3 ± 1.30	9.2 ± 1.64	3	A–B: irregular laths, granular surface; porous.
				G–H: sharp-edged lamels, alveolar-like pattern mixed with smooth blocks.
				I: exposed laths with sharp, irregular surfaces.
1930	10.8 ± 0.80	9.3 ± 0.83	3	G–I: alveolar pattern dominates.
2030	9.0 ± 1.16	8.4 ± 0.86	3	
2130	11.6 ± 0.87	10.0 ± 0.95	3	
2230	10.6 ± 0.15	8.8 ± 0.00	3	A–B: irregular surface, porous, fragments, granules.
2330	11.0 ± 1.88	9.2 ± 0.93	3	C: smooth surface with scattered fragments, some granulate.
				G–H: alveolar, porous, blocky. I: alveolar rare.
0030	11.1 ± 0.20	8.8 ± 0.58	3	I: no alveolar or rare.
0130	10.4 ± 0.94	8.8 ± 1.14	3	
0230	11.0 ± 0.60	9.3 ± 0.53	3	G–H: alveolar with thick strands, blocks.
				I: deep alveolar structure.
0330	9.8 ± 3.00	8.1 ± 0.51	3	G–H: alveolar, lamels not readily discernible.
0430	11.5 ± 0.45	9.7 ± 0.50	3	D–F: lamels vague, short, sharp tips.
0630	11.9 ± 0.98	10.0 ± 1.05	3	
0730	10.7 ± 0.38	9.1 ± 0.45	3	
0830	11.1 ± 1.30	9.3 ± 0.98	3	
0930	10.3 ± 0.77	8.7 ± 1.10	3	
1030	11.1 ± 1.55	9.6 ± 1.31	3	I: no alveolar structures, smooth.
1130	10.9 ± 0.90	9.2 ± 0.88	3	I: heavy alveolar structures with deep pits.
1230	11.4 ± 0.56	9.5 ± 0.68	3	

organic matrix behind, a series of three recently shucked bivalve shells (L = 18.0–28.8 mm; Table 2) (sampled 5 June 1985) were subjected to a 30-sec treatment in 50% hydrochloric acid followed by a distilled water rinse and preparation for SEM.

Another series of three shucked valves (from the 7-day dissolution study), with valves showing reticulated structures, were subjected to a 5-min treatment in 5.25% sodium hypochlorite (commercial Clorox®) followed by distilled water rinses and preparation for SEM.

RESULTS

After a 3-week period, a sudden electrical power surge brought the 31°C "fed" aquarium up to 37°C. This resulted in physiologically stressed clams in this tank within the next 7 days. All clams that remained alive in each of the other tanks were sacrificed at the end of the 7th day in the 4th week. All clams in the ambient tanks, fed and nonfed, maintained a purple-brown highlighted internal shell coloration with a characteristic internal complex crossed-lamellar shell (*i.e.*, internal to pallial line) (Figure 1). Five of the six clams maintained through death or impending death in the hot, "fed" tank produced white internal shell surfaces with crossed-acicular patterns replacing the internal complex crossed-lamellar microstructure (Figure 2). A single clam in the warm, nonfed tank produced a white internal shell with "crossed-acicular" patterns, but all others had "normal" pigmentation and microstructure.

Table 2

Dates and sizes from 7-day dissolution study of *Corbicula fluminea*. Three specimens from each daily sample were examined via scanning electron microscopy. Year = 1984; measurements in mm.

Date	Length ± 1 SD	Width ± 1 SD	Height ± 1 SD
11 November	12.4 ± 2.55	7.8 ± 1.93	9.8 ± 1.36
12 November	11.9 ± 1.62	7.0 ± 0.87	10.1 ± 1.52
13 November	11.9 ± 1.72	7.5 ± 0.67	9.6 ± 1.35
14 November	11.6 ± 1.27	7.1 ± 0.85	8.7 ± 2.20
15 November	11.4 ± 2.34	8.0 ± 2.75	9.5 ± 2.86
16 November	11.5 ± 3.16	6.9 ± 1.99	9.8 ± 1.57
17 November	11.6 ± 1.72	7.0 ± 1.09	10.1 ± 2.57
18 November	12.3 ± 2.69	7.7 ± 2.12	9.4 ± 1.46
19 November*	11.7 ± 1.81	6.9 ± 1.29	

* Dead upon opening at termination of experiment.

Forced Adduction

24-h study (see Table 1): Internal to the pallial line after 16 h of forced adduction, obvious changes in shell microstructure occurred. These changes included increased porosity of organic layers in cross-lamellar structures (Figure 3), disruption of regular lamel tips (Figure 4), and finally a breakdown of organized lath orientation (Figures 5, 6). In some cases this type of dissolution or disruption of internal shell surface microstructure resembles a crossed-acicular pattern.

7-day study: During the first 5 days of forced adduction there was no mortality. All 10 clams sampled daily were alive up to day 6. On day 6, all 10 clams sampled were dead and on day 7, only 2 of 10 sampled were alive.

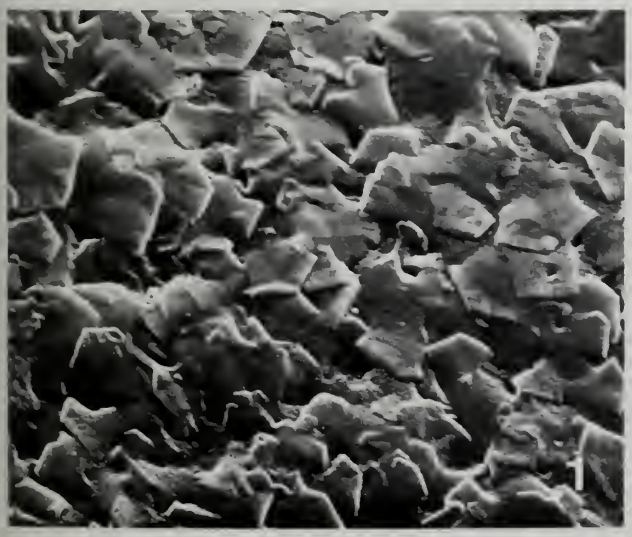
By the 7th day of forced adduction, live clams showed considerable disruption of internal shell microstructure. In the central portion of the internal shell, there was little organization of calcareous structures. Instead, a reticulated microstructural pattern of apparently high organic material was present (Figure 7). This obscured any organized microstructure that might have otherwise been present beneath the eroded surface.

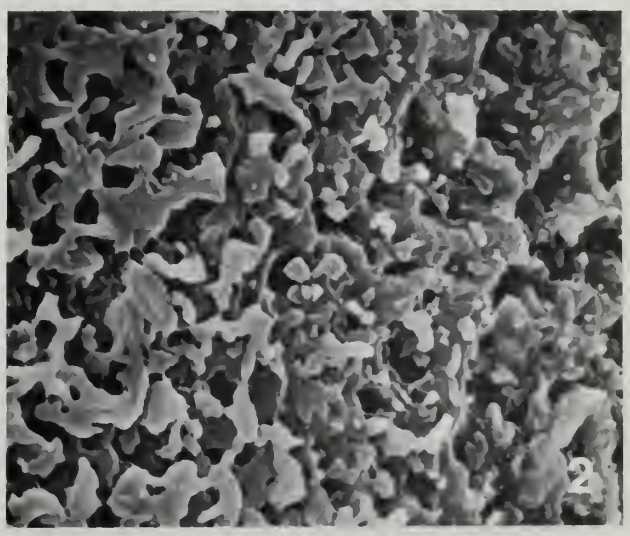
In specimens treated for 30 sec with a 50% solution of hydrochloric acid, a pattern of microstructures similar to the reticulate pattern noted above was obtained (Figure 8). A reticulate matrix high in organic material remained after apparent dissolution of calcareous features. Following treatment with an organic solvent (*i.e.*, sodium hypochlorite), a smooth surface remained.

Field Controls

Clams brought into the laboratory alive but apparently in an "unhealthy" condition (*i.e.*, weak adduction response, sluggish foot activity) showed pure white internal shell coloration and typically an internal shell microstructure that resembled crossed-acicular (or an eroded form of complex crossed-lamellar).

All clams examined directly from the field in healthy condition (*i.e.*, rapid adduction response, active pedal movement, rapid burrowing) showed internal shells with purple highlights and a typical complex crossed-lamellar microstructure internal to the pallial line (see Prezant & Tan Tiu, 1985).

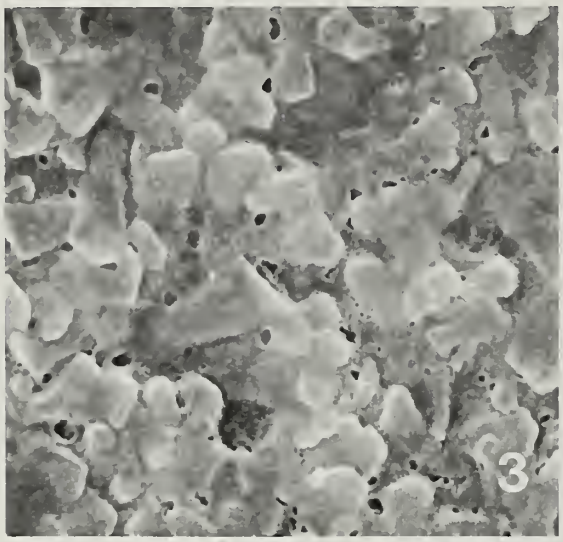




Explanation of Figures 1 and 2

Figure 1. Surficial view of complex crossed-lamellar lath tips in "normal" shell of *Corbicula fluminea*. [All photographs are scanning electron micrographs.] Horizontal field width = 2 μm.

Figure 2. "Crossed-acicular" microstructure induced by subjecting small *C. fluminea* specimens to warm, high organic waters followed by a lethal rise in aquarium temperatures. Horizontal field width = 2 μm.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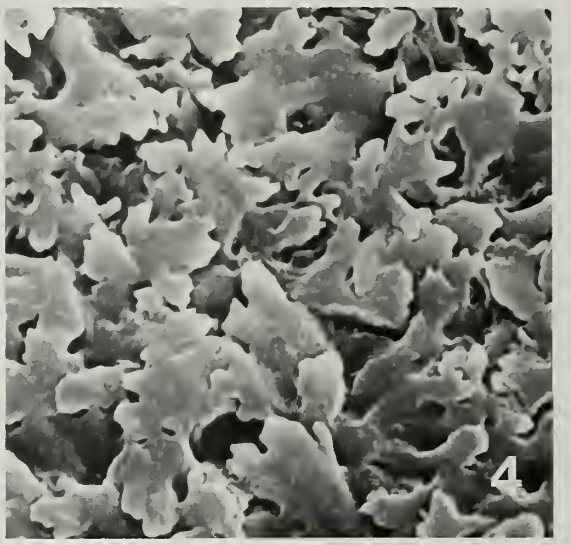
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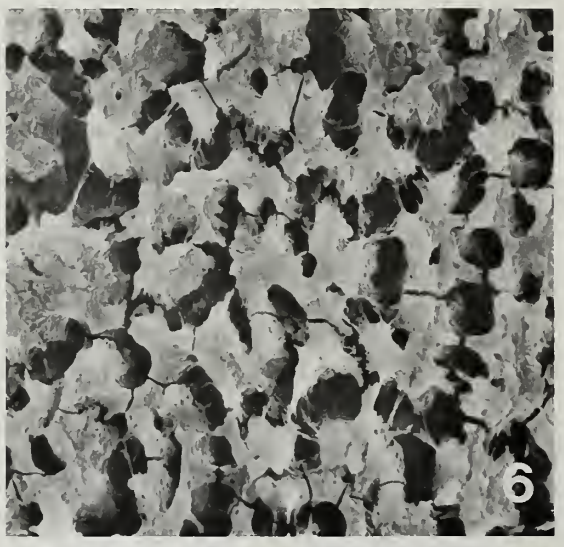
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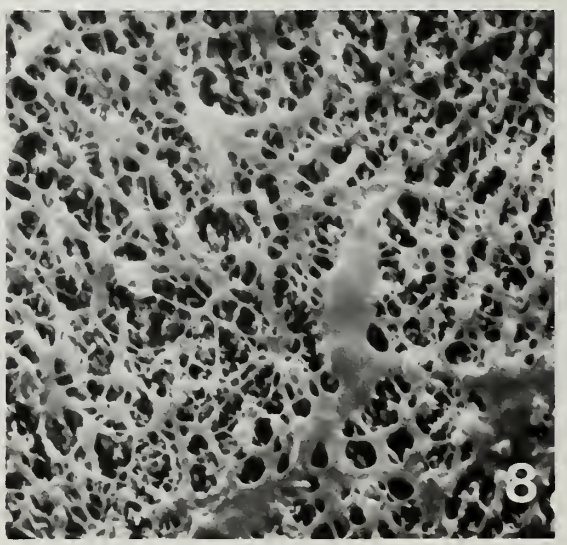
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DISCUSSION

The surficial microstructures of complex crossed-lamellar layers are often irregularly arranged. TAYLOR *et al.* (1969) have noted several bivalve species that have surficial complex crossed-lamellar microstructures that have a "confused surface pattern." In these the second-order lamels "vary in attitude" creating third-order lamels with an apparent random orientation. The physiological status of specimens examined by TAYLOR *et al.* (1969) was not documented. A discussion of variation in complex crossed-lamellar structures can be found in TAYLOR *et al.* (1969) and CARTER (1980a).

CARTER (1980b) defines crossed-acicular microstructures as similar to crossed-lamellar "except that each aggregation consists of only a few parallel elongate subunits." The conversion of crossed-lamellar internal shell microstructures to "crossed-acicular" microstructures (in essence nondiscernible from some erosive patterns shown by CRENSHAW [1980]) raises interesting questions concerning nomenclatural validity of specific crossed-lamellar microstructures. In *Corbicula fluminea* it appears that crossed-acicular microstructures are an aberrant form of complex crossed-lamellar microstructures with the irregularity of laths being either (1) a modification of the typical shell microstructure, or (2) a new type of deposit produced under specific conditions, or (3) the result of dissolution phenomena. It is difficult to assume that the crossed-acicular-like deposits are the result of usual erosive events, as no erosive pitting was evident nor was this type of microstructure consistently found in bivalves subjected to forced adduction. Instead, a more erosive type of dissolution surface was present inside the valves of specimens that were forced to remain closed for long periods. In specimens that were clamped for up to 7 days, the internal shell microstructure bore little resemblance to the crossed-acicular pattern. The build-up of acids in the extrapallial fluid during adduction seemingly impinges first upon the calcified microstructures and leaves an organic residue behind. This is indeed what is typically seen in long-term adducted specimens we examined and is considered predictable. (For example, CURREY [1988] briefly discusses the erosive resistance of "conchiolin," at least in deterring some drilling predators; see also LEWY & SAMTLEBEN [1979].) In shorter-term studies (*i.e.*, 24 h) with *Corbicula*, we found microstructures that at least broadly resembled crossed-acicular patterns.

TAN TIU (1987) observed that valves of recently sacrificed *Corbicula fluminea* placed in the Leaf River and Eddy Lake of Mississippi for at least 3 months also had white internal shell coloration but lacked crossed-acicular patterns. Shell microstructures dominating were primarily elongate structures resembling remnants of dissolution in non-living systems. This indicates that crossed-acicular patterns found in *C. fluminea* from empty shells collected along the shore could have been formed prior to the death of the animal. Moreover, in longer-term thermal and trophic experiments (Prezant & Tan Tiu, unpublished data), not all internal shell surfaces of dead clams were white and no crossed-acicular microstructures were observed. TAN TIU (1987) did observe crossed-acicular microstructures in clams collected live from the Leaf River but only rarely (*i.e.*, 1 of 30 in September 1985, 9 of 28 in October 1985, and 2 of 30 in March 1986). These conflicting data make our present results equivocal and we have yet to discern the exact cause of the modified shell.

CRENSHAW & NEFF (1969) and CRENSHAW (1980) demonstrated distinct differences in interior shell surfaces proximal to the pallial line of *Mercenaria mercenaria* (Linnaeus) following emergence from water for 3 h. They found that following emersion, crystals were "poorly organized with large voids on the inner surface" while those outside the pallial line retained "sharp edges" and organization and filled "available space." CRENSHAW (1980) noted, however, that microstructures inside and outside the pallial line in *M. mercenaria* are normally different (as they are in *Corbicula fluminea*) with the outer shell dominated by crossed-lamellar and prismatic, and the inner shell consisting of complex crossed-lamellar and/or homogeneous microstructures. CRENSHAW (1980) characterized the shell found inside the pallial line after aerial exposure as characteristic of erosive dissolution that occurs during anaerobiosis with the build-up of acids in the extrapallial fluid. This same argument can be made for *C. fluminea* if we could be sure that anaerobiosis was the stimulus. In our experiments, stressed clams usually remained slightly abducted and this could preclude the build-

←

Explanation of Figures 3 to 8

Figure 3. During 24 h of forced adduction, bivalves (*Corbicula fluminea*) frequently showed increased porosity of organic layers surrounding lamel tips. Horizontal field width = 2 μm.

Figure 4. During 24-h forced adduction studies, lamel tips were often disrupted and showed dendritic qualities. Horizontal field width = 2 μm.

Figure 5. Final phases in 24-h adduction dissolution studies revealed microstructures that had complete disruption of organized lamels and microstructurally resembled a stage intermediate between crossed-acicular patterns and complete dissolution patterns (see Figures 2, 6). Horizontal field width = 2 μm.

Figure 6. Complete disruption of organized lamels results after 24 h of forced adduction. Horizontal field width = 10 μm.

Figure 7. After 7 days of forced adduction, bivalves showed a reticulate pattern of apparently organic material in the central portion of the shell interior. Horizontal field width = 2 μm.

Figure 8. Central interior of the shell of a specimen of *C. fluminea* treated for 30 sec with 50% hydrochloric acid. The resulting reticulate pattern resembles the pattern seen in Figure 7. Horizontal field width = 2 μm.

up of erosive acids in the extrapallial space. In addition, CRENSHAW & NEFF (1969) found that dissolution probably was a rapid result of anaerobiosis and thus erosion should begin quickly. Specimens of *C. fluminea* stressed by forced adduction showed similar signs of modified internal shell as in clams that were experimentally stressed by heat and organic water load over longer periods of time (*i.e.,* 24 h force adducted vs. several days in warm, high organic waters) (latter from unpublished data, Prezant, Tan Tiu and Chalermwat). Micrographs shown by CRENSHAW (1980) of complex crossed-lamellar shell of *Mercenaria mercenaria* that had undergone dissolution are reminiscent of modified *Corbicula* shell resembling crossed-acicular. In *Mercenaria,* however, the pattern shows fewer elongate units. If any of our specimens that showed crossed-acicular patterns were physiologically stressed, the appearance of a porous microstructure (showing gaps in organic deposits) could be envisioned as being energy efficient. The erosion of a complex crossed-lamellar microstructure in an "inactive" extrapallial fluid or conchiolin base can also be envisioned as energy saving. These patterns of shell deposition or shell dissolution are distinct from the eroded internal shell seen after 7 days of forced adduction. It is possible that the two forms are a continuum of each other (*i.e.,* phases of progressive dissolution). We suggest that the internal shell surface seen after 7 days of adduction represents strongly eroded shell (compare with HCl-treated shell) that has had most surficial calcareous material dissolved. The crossed-acicular-like microstructure either is a "milder" type of erosive pattern (induced by lower stress without the build up of high concentrations of erosive extrapallial fluid acids) or a metabolically inexpensive form of shell deposition (low in organics).

It is possible that the organism produces the modified complex crossed-lamellar structures as a result of a shift in body energetics. Thus far there is no definitive work that has discerned the energy costs of producing molluscan shell, in particular the partitioned costs of producing the calcium carbonate portion versus the organic matrix. CURREY (1988) reviews the little that is known of this subject and briefly discusses the work of PALMER (1983) that indicates a higher energy cost for producing the organic portion of shell. Under stressed conditions mollusks could shift energy reserves toward life-sustaining functions, which may not include shell production in post-larval animals. Thus, under stress the bivalve could terminate normal shunting of incipient shell materials through the mantle, thereby producing a modified extrapallial fluid that could be conducive to modified shell production. Chalky deposits seen in ostreid bivalves are reminiscent of this situation. CARRIKER *et al.* (1980) and STENZEL (1971) point out that chalky shell deposits are composed of less calcareous material than a comparable shell volume of typical foliated structure. The supposition is that chalky deposits are more economical to produce than more compact, regular foliated shell. If shell organic matrix (*i.e.,* conchiolin) is energetically more expensive to produce in corbiculid and other bivalves, perhaps we need to look towards temporal modifications of the type of organic material being produced under given circumstances to account for differences in shell microstructure.

The origin of the modified "complex crossed-acicular" shell microstructure we found using stressed *Corbicula fluminea* remains unclear. We must exercise extreme care, however, in separating a crossed-acicular microstructure from the erosive remains of a crossed-lamellar microstructure. We might speculate here that stress in some instances will induce internal shell erosion; in others stress could produce replacement deposition in the form of an energetically cheaper shell microstructure.

Very little is known about the influence that environment has on biomineralization or crystallization in mollusk shell. Since different environmental regimes produce different growth rates (MALONE & DODD, 1967) it is likely that these variations will be reflected in shell microstructure. TAN TIU (1988), for instance, has found significant temporal (seasonal) changes in shell microstructure within the bivalve *Polymesoda caroliniana* (Bosc). Subtle variations in shell microstructure in *Corbicula fluminea* can be induced by variation in microhabitat in conjunction with the bivalve's physiological condition.

Variations in dissolution and deposition patterns lead to a wide variety of microstructural forms. To extrapolate our present data on internal shell color and microstructure to help decipher the taxonomic quagmire developed in the debate over the number of species of North American *Corbicula* would be premature. This is particularly true in light of our equivocal results based on the present report and unpublished data. The debate continues but we argue strongly to limit our discussions to valid taxonomic characters and move away from shell color and subtle shell morphometrics.

ACKNOWLEDGMENTS

We acknowledge the kind help of Dr. Raymond Scheetz and Mr. Thomas Pittman in the operation of the SEM, and Mr. Thomas Rogge who helped with some of the collections. Comments by Drs. J. G. Carter, R. F. McMahon, and A. R. Palmer substantially improved this manuscript. This research was supported in part by a University of Southern Mississippi Development Grant (to RSP) and a National Capital Shell Club Scholarship (to ATT).

LITERATURE CITED

BRITTON, J. C. 1982. Biogeography and ecology of the Asiatic clam, *Corbicula* in Texas. Pp. 21–31. *In:* J. R. Davis (ed.), Proceedings of the Symposium on Recent Benthological Investigations in Texas and Adjacent States. Aquatic Sciences Section. Texas Academy of Science. San Angelo.

BRITTON, J. C. & B. MORTON. 1979. *Corbicula* in North America: the evidence reviewed and evaluated. Pp. 249–287. *In:* J. C. Britton (ed.), Proceedings of the First International

Corbicula Symposium, Texas Christian University. Fort Worth.

CARRIKER, M. R., R. E. PALMER & R. S. PREZANT. 1980. Functional ultramorphology of the dissoconch valves of the oyster *Crassostrea virginica*. Proc. Natl. Shellfish. Assoc. 70: 139–183.

CARTER, J. G. 1980a. Environmental and biological controls of Bivalve shell mineralogy and microstructure. Pp. 69–113. *In:* D. C. Rhoads & R. A. Lutz (eds.), Skeletal growth of aquatic organisms. Plenum Publishing Corp.: New York.

CARTER, J. G. 1980b. Bivalve shell mineralogy and microstructure. Selected mineralogical data for the Bivalvia. Pp. 627–673. *In:* D. C. Rhoads & R. A. Lutz (eds.), Skeletal growth of aquatic organisms. Appendix 2. Plenum Publishing Corp.: New York.

COUNTS, C. L., III. 1986. The zoogeography and history of the invasion in the United States by *Corbicula fluminea* (Bivalvia: Corbiculidae). *In:* J. C. Britton (ed.), Proceedings of the Second International *Corbicula* Symposium. Amer. Malacol. Bull., Spec. Ed. 2:7–39.

CRENSHAW, M. A. 1980. Mechanisms of shell formation and dissolution. Pp. 115–132. *In:* D. C. Rhoads & R. A. Lutz (eds.), Skeletal growth of aquatic organisms. Plenum Press: New York.

CRENSHAW, M. A. & J. M. NEFF. 1969. Decalcification at the mantle-shell interface in molluscs. Amer. Zool. 9:881–885.

CURREY, J. D. 1988. Shell form and strength. Pp. 183–210. *In:* E. R. Trueman & M. R. Clarke (eds.), The Mollusca. Vol. 11. Academic Press: San Diego, CA.

HILLIS, D. M. & J. C. PATTON. 1979. Morphological and electrophoretic evidence for two species of *Corbicula* (Bivalvia: Corbiculidae) in North America. Amer. Midl. Natur. 108:74–80.

LEWY, Z. & C. SAMTLEBEN. 1979. Functional morphology and palaeontological significance of conchiolin layers in corbulid pelecypods. Lethaia 12:341–351.

MALONE, P. G. & J. R. DODD. 1967. Temperature and salinity effects on calcification rate in *Mytilus edulis* and its paleoecological implications. Limnol. Oceanogr. 12:432–436.

MCLEOD, M. J. 1986. Electrophoretic variation in U.S. *Corbicula*. *In:* J. C. Britton (ed.), Proceedings of the Second International *Corbicula* Symposium. Amer. Malacol. Bull., Spec. Ed. 2:125–132.

MCMAHON, R. F. 1982. The occurrence and spread of the introduced Asiatic freshwater clam, *Corbicula fluminea* (Müller), in North America: 1924–1982. Nautilus 96:134–141.

MORTON, B. 1986. *Corbicula* in Asia—an updated synthesis. *In:* J. C. Britton (ed.), Proceedings of the Second International *Corbicula* Symposium. Amer. Malacol. Bull., Spec. Ed. 2:113–124.

PALMER, A. R. 1983. Relative cost of producing skeletal organic matrix versus calcification: evidence from marine gastropods. Mar. Biol. 75:287–292.

PRASHAD, B. 1929. Revision of the Asiatic species of *Corbicula* II. I. The Indian species of *Corbicula*. Memoirs, Indian Museum 9:29–48.

PREZANT, R. S. & A. TAN TIU. 1985. Comparative shell microstructure of North American *Corbicula* (Bivalvia: Sphaeriacea). Veliger 27:312–319.

PREZANT, R. S. & A. TAN TIU. 1986. Spiral crossed-lamellar shell growth in the bivalve *Corbicula* (Mollusca: Bivalvia). Trans. Amer. Microsc. Soc. 105:338–347.

SINCLAIR, R. M. & B. G. ISOM. 1963. Further studies on the introduced Asiatic clam *Corbicula* in Tennessee. Tennessee Pollution Control Board, Tennessee Department of Public Health, Nashville, Tennessee. 76 pp.

STENZEL, H. B. 1971. Oyster. Pp. N953–N1224. *In:* R. C. Moore (ed.), Treatise on invertebrate paleontology. Part n, Vol. 3, Mollusca 6, Bivalvia. Geological Society of America and University of Kansas: Lawrence.

TAN TIU, A. 1987. Influence of environment on shell microstructure of *Corbicula fluminea* and *Polymesoda caroliniana* (Bivalvia: Heterodonta). Ph.D. Dissertation, University of Southern Mississippi, Hattiesburg. 148 pp.

TAN TIU, A. 1988. Temporal and spatial variation of shell microstructure of *Polymesoda caroliniana* (Bivalvia: Heterodonta). Amer. Malacol. Bull. 6(2):199–206.

TAYLOR, J. D., W. J. KENNEDY & A. HALL. 1969. The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea–Trigonacea. Bull. Brit. Mus. (Natur. Hist.) Zool., Suppl. 3. 125 pp., 29 plates.

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Studies on Olividae. VIII. Protoconch Measurements as Supraspecific Characters in the Family Olividae

by

B. TURSCH

Collectif de Bio-Ecologie, Faculté des Sciences, Université Libre de Bruxelles,
50, av. F.D. Roosevelt, 1050 Brussels, Belgium

Abstract. Data on 87 taxa indicate that protoconch measurements are efficient supraspecific characters in the family Olividae.

INTRODUCTION

Olive shells are difficult to describe in words because they do not possess obvious, clear-cut conchological discriminating features. They are devoid of sculpture and many are of rather uniform shape. Columellar plications are often quite complex, irregular in shape, and variable. When present, color patterns are often highly variable and their intricacy defies accurate verbal description. In some cases the worded descriptions utilized so far do not transmit relevant taxonomic information. Without reference to types or illustrations many species of *Oliva* simply cannot be unambiguously recognized from their original description (often written in the language of the art critic rather than that of the scientist). In addition, the great variability of many olive shells is a familiar problem to malacologists: it is often difficult to draw sharp and stable boundaries between taxa.

The problems prevailing at the species level are logically expected to be reflected at the upper taxonomic levels. There has been no recent critical review of the supraspecific grouping of the family Olividae as a whole. For lack of better choice, the divisions adopted in the latest revision (PETUCH & SARGENT, 1986) have been followed hereunder.

As long as objective discriminant characters (and the limits of their variation) are not clearly defined, the classification of Olividae is bound to remain largely a question of personal opinion. The use of reliable, quantitative characters would certainly help to clear some of that systematic confusion. In an attempt to provide such taxonomic tools, a set of 13 protoconch measurements has been defined by TURSCH & GERMAIN (1985, 1986a) together with some other quantitative shell characters. These protoconch characters have been shown to be useful and reliable both at the subspecific (TURSCH *et al.,* 1986a) and the specific (TURSCH *et al.,* 1986b) levels in the genus *Oliva.* No data justifying their use at the supraspecific level have been provided so far.

Protoconch measurements cannot always be utilized as identification characters because the apex of many olive shells is quite fragile and often found missing or damaged (this is probably due to rough handling as the percentage of shells with intact protoconch is much higher in self-collected material than in museum or commercial specimens). On the other hand, protoconch data do not vary with the size of the specimen. They allow easy comparison of adult with juvenile shells, can be utilized for fossil material, and are thus very attractive for systematic work.

The taxonomic importance of the protoconch has not escaped the notice of other students of Olividae. In their recent revision of the genus *Oliva,* PETUCH & SARGENT (1986) state: "Because this is such a specific character, the protoconch should be considered the most important means of differentiating species within genus and subgenus groups." Very brief references to the size (and sometimes the general shape) of the protoconch can indeed be found for 22 of the 176 taxa described in that work. Protoconch characters have also been utilized at the specific level in the genus *Agaronia* (LOPEZ *et al.,* 1988).

Can protoconch measurements be utilized at the supraspecific level in the family Olividae? The statement of PETUCH & SARGENT (1986) reproduced here above explicitly restricts the use of protoconch characters to the specific level. The authors do not use these characters in the definition of any of the 19 subgenera (10 being newly created) they recognize in the genus *Oliva.* On the other hand, protoconch size has been utilized as a supraspecific character in Ancillinae by KILBURN (1977). The general uniformity of the protoconch within the genus *Ancilla* is also reported (and illustrated for many species) by KILBURN (1981).

The present work is a preliminary survey of protoconch morphology trends in the family Olividae. Its sole purpose is to test the taxonomic potential of some protoconch measurements as supraspecific characters in the family Olividae.

MEASUREMENTS

In order to keep this paper within reasonable size limits, only three very simple measurements (**nw**, **lpro**, **spro**) have been utilized. These measurements are justified and defined in detail in TURSCH & GERMAIN (1985). All protoconch measurements are performed using a dissecting microscope at suitable magnification. The measurement **nw** is the number of volutions of the protoconch. The transition from protoconch to teleoconch is carefully determined and marked with removable ink. The determination of the transition is straightforward in most *Oliva* but sometimes more difficult in other groups. Discontinuities in the suture and changes of curvature of the whorl are then of great assistance. The shell is then properly oriented and the angular position of the mark relative to the reference axes of the ocular reticulum is easily determined to the nearest 18°. The quantity **nw** can thus be measured to the nearest 0.05 whorl. The suture of the early whorls is then carefully drawn with the help of the camera lucida attachment of the microscope. A 1-mm reference length (predetermined on the ocular reticulum) is also drawn. The measurements **spro** (the diameter of the nucleus) and **lpro** (the diameter of the protoconch at one and one-half volution) are thus easily made. The meaning of **lpro** and **spro** is evident from Figure 1. The quantity (**lpro** − **spro**) reflects the rate of expansion of the spiral in the plane perpendicular to the axis of the shell. The quantities **nw** and (**lpro** − **spro**) are *a priori* independent characters.

One will note that the above protoconch measurements differ from some in common use. The choice of the method, its accuracy, and precision are discussed in TURSCH & GERMAIN (1985). One will also note that the above measurements determine neither the shape nor the size of the protoconch.

MATERIAL EXAMINED

In the genus *Oliva* 47 species were selected at random with the only constraint being that 12 taxa (26%) were chosen in the Panamic-Atlantic region, in order to approximate the real distribution of species (Table 1). Species from that zone amount to 14 (25%) of the 57 species recognized by ZEIGLER & PORRECA (1969) and 43 (24%) of the 176 species recognized by PETUCH & SARGENT (1986). In the other genera, selection of the sample was very much influenced by the availability of specimens with the protoconch intact. The problem was often compounded by the fact that the protoconch of many species is very difficult to measure; these taxa were not considered. The initial aim was to measure five specimens of every species. This could not always be achieved for lack of available intact specimens.

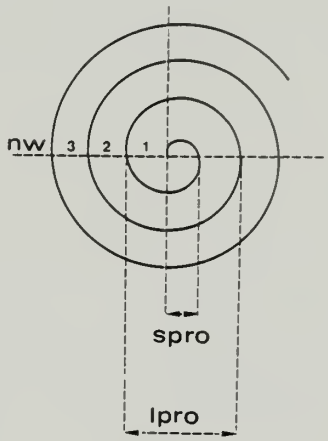

Figure 1

Top view of a fictive protoconch: **nw**, **lpro**, and **spro**.

The list hereunder does not endorse the correctness and the validity of all the taxa. Some names are used with great reluctance.

Abbreviations: AM, refers to specimens from the Instituut voor Taxonomische Zoölogie (Zoölogische Museum, Amsterdam); DG, to the D. Greifeneder collection (Schwenningen); FN, to the F. Nolf collection (Ostende); JS, to the J. Senders collection (Brussels); RM, to the R. Martin collection (Cebu); and BT, to the B. Tursch collection (Brussels).

Subfamily OLIVINAE

Genus *Agaronia*

A. acuminata boavistensis Burnay & da Conceiçao, 1986. CABO VERDE: BT-1212 (Sal Rei, Boavista I.), BT-5893, BT-5894, and BT-5896 (no loc.). *A. propatula* Conrad, 1849. COSTA RICA (Playa de Jascos): BT-5897, BT-5898, BT-5899, and BT-5900. *A. travassosi* Lange de Morretes, 1938. BRASIL (off Cabo Frio): BT-2926, BT-3270, BT-3277, and BT-4070.

Genus *Oliva*

O. amethystina Röding, 1798. For this species see TURSCH *et al.*, 1986b. AUSTRALIA (Queensland, Bowen): DG-3670/5; PHILIPPINES: DG-0253 (Sulu) and DG-0995 (Cebu); SOLOMONS (Langa-Langa): DG-2525/6; TAHITI (Faaone): DG-1719/b. *O. arctata* Marrat, 1871. THAILAND: BT-1232 and BT-0081 (no loc.); BT-3940 and BT-3942 (off Ranong); BT-3947 (off Kor Raya Is.). *O. australis* Duclos, 1835. S. AUSTRALIA: BT-1475 and BT-1478 (no loc.); BT-3603 (Elliston Bay); BT-4506 (Yorke Peninsula); BT-3600 (Brighton Reef). *O. buelowi* Sowerby, 1888. PAPUA NEW GUINEA (Hansa Bay, Laing Is.): BT-0422, BT-0423, BT-0424, BT-0425, and BT-0426. *O. bulbiformis* Duclos, 1835. INDONESIA (Bali): JS-028, JS-029, BT-1549, and BT-1551. PHILIPPINES (Bohol): BT-1556. *O. bulbosa* Röding, 1798. ABU DHABI: BT-4604, BT-4605, BT-4606, BT-4607, and BT-4608. *O. caerulea* Röding, 1798. INDONESIA (Bali): BT-0451, BT-

Table 1

Taxa examined.

Subfamily OLIVINAE

Genus *Agaronia*

A. acuminata boavistensis Burnay & da Conceiçao, 1986.
A. propatula Conrad, 1849.
A. travassosi Lange de Morretes, 1938.

Genus *Oliva*

O. amethystina Röding, 1798.
O. arctata Marrat, 1871.
O. australis Duclos, 1835.
O. buelowi Sowerby, 1888.
O. bulbiformis Duclos, 1835.
O. bulbosa Röding, 1798.
O. caerulea Röding, 1798.
O. caldania Duclos, 1835.
O. carneola Gmelin, 1791.
O. caroliniana Duclos, 1835.
O. concinna Marrat, 1871 (of authors).
O. dubia Schepman, 1911.
O. flammulata Lamarck, 1811.
O. hirasei Kuroda & Habe, 1952.
O. fulgurator Röding, 1798.
O. kaleontina Duclos, 1835.
O. lacanientai Greifeneder & Blöcher, 1985.
O. lenhilli Petuch & Sargent, 1986.
O. lignaria Marrat, 1868.
O. mantichora Duclos, 1835.
O. miniacea Röding, 1798.
O. neostina Duclos, 1835.
O. oliva L., 1758 (of authors).
O. ornata Marrat, 1867.
O. parkinsoni Prior, 1975.
O. paxillus Reeve, 1850.
O. polpasta Duclos, 1835.
O. porphyria L., 1758.
O. reclusa Marrat, 1871.
O. reticularis Lamarck, 1811.
O. reticulata Röding, 1798.
O. rubrolabiata Fischer, 1902.
O. rubrofulgurata Schepman, 1911.
O. rufula Duclos, 1835.
O. sayana Ravenel, 1834.
O. scripta Lamarck, 1811.
O. semmelincki Schepman, 1911.
O. sericea Röding, 1798.
O. sidelia Duclos, 1835.
O. spicata Röding, 1798.
O. splendidula Sowerby, 1825.
O. taeniata Link, 1807.
O. tesselata Lamarck, 1811.
O. tricolor Lamarck, 1811.
O. undatella Lamarck, 1811.
O. vidua Röding, 1798.
O. williamsi Melvill & Standen, 1897.

Genus *Olivancillaria*

O. contortuplicata Reeve, 1850.
O. urceus Röding, 1798.
O. uretai Klappenbach, 1965.
O. vesica vesica Gmelin, 1791.

Subfamily OLIVELLINAE

Genus *Olivella* s.l.

O. anazora Duclos, 1835.

Table 1

Continued.

O. gracilis Broderip and Sowerby, 1829.
O. japonica Pilsbry, 1895.
O. pulchella Duclos, 1835.
O. volutella Lamarck, 1811.
O. zanoeta Duclos, 1835.
O. zonalis Lamarck, 1811.

Subfamily ANCILLINAE

Ancilla (*Sparellina*) *acuminata* Sowerby, 1859.
Ancilla (*Sparellina*) *ampla* Gmelin, 1791.
Baryspira australis Sowerby, 1830.
Ancillus buccinoides Lamarck, 1803.
Ancillarina canalifera Lamarck, 1802.
Ancilla (*Sparella*) *castanea* Sowerby, 1830.
Ancillista cingulata Sowerby, 1830.
Ancilla cinnamomea Lamarck, 1801.
Baryspira depressa Sowerby, 1859.
Amalda (?) *dimidiata* Sowerby, 1850.
Alocospira (?) *edithae* Pritchard & Gatliff, 1898.
Eburna glabrata L., 1758.
Eburna lienardi Bernardi, 1821.
Ancilla (*Sparellina*) *lineolata* A. Adams, 1853.
Alocospira (*s.l.*) *marginata* Lamarck, 1810.
Ancilla (*Hesperancilla*) *matthewsi* Burch and Burch, 1967.
Alocospira (*s.l.*) *monolifera* Reeve, 1864.
Ancillista muscae Pilsbry, 1826.
Gracilispira novaezelandiae Sowerby, 1859.
Ancilla (*Sparellina*) *ovalis* Sowerby, 1859.
Ancillus olivula Lamarck, 1803.
Alocospira (*s.l.*) *rosea* Macpherson, 1951.
Ancilla (*Sparella*) *sarda* Reeve, 1864.
Amalda tankervillii Swainson, 1825.
Ancillista velesiana Iredale, 1936.
Ancilla (*Sparella*) *ventricosa* Lamarck, 1811.

0452, BT-0454, BT-455, and BT-1987. *O. caldania* Duclos, 1835. AUSTRALIA (Queensland, no loc.): BT-1607, BT-1609, BT-1611, BT-1612, and BT-1614. *O. carneola* Gmelin, 1791. SOLOMON Is.: BT-0301 (Guadalcanal); BT-2516 (Langa-langa); BT-2548, BT-2549, and BT-2553 (no loc.). *O. caroliniana* Duclos, 1835. MOZAMBIQUE (no loc.): BT-1567. SOUTH AFRICA (Durban): BT-2617, BT-2618, BT-3800, and BT-3997. *O. concinna* Marrat, 1871 (of authors). This is the taxon figured pl.10, figs. 9 and 10 in PETUCH & SARGENT (1986) and pl.10, fig. 3 in ZEIGLER & PORRECA (1969). NEW HEBRIDES (Port Vila): BT-4343. SOLOMONS: BT-2440 and BT-2441 (Honiara); BT-4438 (Guadalcanal); BT-4342 (no loc.). *O. dubia* Schepman, 1911. PAPUA NEW GUINEA (Hansa Bay, Laing Is.): BT-4928, BT-4929, BT-4930, and BT-4931. PHILIPPINES (Bohol): RM-0017. *O. flammulata* Lamarck, 1811. GABON (Port Gentil): BT-2087 and BT-2088. MAURITANIA (La Awera): BT-4215. SENEGAL (Dakar): BT-2127 and BT-4432. *O. fulgurator* Röding, 1798. ARUBA: AM-10, AM-33, and AM-11 (no loc.); BT-3420 (off Malmok). VENEZUELA (La Guayra): Am-01. *O. hirasei* Kuroda & Habe, 1952. PHILIPPINES (Sulu): BT-5021, BT-5022, BT-5023, BT-5024, and BT-5025. *O. kaleontina* Duclos, 1835. GALAPAGOS (St. James): BT-4225. PANAMA (Cebaco Is.): BT-3751, BT-3752, BG-3753, and BT-3756. *O. lacanientai* Greifeneder & Blöcher, 1985. PHILIPPINES (off Cebu, 250–300 m): BT-5045, BT-5046, BT-5047, BT-5048, and BT-5049. *O. lenhilli* Petuch & Sargent, 1986. PHILIPPINES (off Bohol, 100 m): RM-003, RM-005, RM-006, RM-008, and RM-009. *O. lignaria* Marrat, 1868. W.

Australia: BT-4831 and BT-4832 (Northwest Cape); BT-3206, BT-3207, and BT-3208 (Broome). *O. mantichora* Duclos, 1835. For this species see Tursch *et al.*, 1986b. Maldives (Ihuru reef): DG-5107/3. Papua New Guinea (Port Moresby): DG-5408/3 and DG-5408/8. Philippines (no loc.): BT-4534 and BT-4545. *O. miniacea* Röding, 1798. Philippines (no loc.): BT-3678, BT-4585, BT-4586, BT-4587, and BT-4588. *O. neostina* Duclos, 1835. Papua New Guinea (Hansa Bay): BT-5016, BT-5017, BT-5018, BT-5019, and BT-5020. *O. oliva* L., 1758 (of authors). This is the taxon figured pl.15, figs. 14 and 15 in Petuch & Sargent (1986). Philippines (no loc.): BT-4589, BT-4590, BT-4591, BT-4592, and BT-4593. *O. ornata* Marrat, 1867. Philippines: FN-64/1 and BT-0387 (no loc.); BT-4243 and BT-4837 (Sulu). *O. parkinsoni* Prior, 1975. Solomons (no loc.): BT-2480, BT-2481, BT-2482, BT-2483, and BT-2485. *O. paxillus* Reeve, 1850. Hawaii: BT-0931 and BT-1928 (Oahu); BT-1931 (Kaui); BT-4314 and BT-4316 (no loc.). *O. polpasta* Duclos, 1835. Mexico: BT-4613 (Oaxaca, off Salina Cruz); BT-0314, BT-0315, and BT-0316 (Baja California). Panama (Kobbe Beach): BT-0363. *O. porphyria* L., 1758. Panama (Cebaco Is.): BT-3717, BT-3722, BT-3723, BT-3724, and BT-3726. *O. reclusa* Marrat, 1871. Aruba (Hadicurari Beach): AM-020, AM-021, AM-022, AM-023, and AM-025. *O. reticularis* Lamarck, 1811. Cuba (Guantanamo): BT-2190, BT-2220, BT-2221, BT-2223, and BT-2666. *O. reticulata* Röding, 1798. Philippines (no loc.): BT-4594, BT-4595, BT-4596, BT-4597, and BT-4598. *O. rubrolabiata* Fischer, 1902. Vanuatu: BT-0100 and BT-5011 (Port Vila); BT-3493 and BT-3994 (off Banks Is.); BT-3959 (Vanuatu). *O. rufofulgurata* Schepman, 1911. Papua New Guinea (Rabaul): BT-3926, BT-3927, BT-4614, BT-4615, and BT-4616. *O. rufula* Duclos, 1835. Papua New Guinea (Hansa Bay): BT-4599, BT-4600, BT-4601, BT-4602, and BT-4603. *O. sayana* Ravenel, 1834. U.S.A. (Florida, Marco Beach): BT-3012, BT-3013, BT-3105, BT-3108, and BT-3113. *O. scripta* Lamarck, 1811. Haiti: BT-3962 and BT-3964 (Gonave Bay); BT-2379 (off S coast). U.S.A. (Florida, Marathon Key): BT-2150 and BT-2154. *O. semmelincki* Schepman, 1911. Papua New Guinea (Hansa Bay): BT-0793, BT-0794, BT-0795, BT-0796, and BT-0797. *O. sericea* Röding, 1798. Indonesia (Bali): BT-0012, BT-0013, BT-2012 and BT-4046. New Caledonia (E coast): BT-3341. *O. sidelia* Duclos, 1835. Seychelles (Mahé): BT-2707, BT-2708, BT-2710, BT-2712, and BT-2714. *O. spicata* Röding, 1798. Panama (Cebaco Is.): BT-3765, BT-3766, BT-3767, BT-3768, and BT-3770. *O. splendidula* Sowerby, 1825. Panama (no loc.): BT-3729, BT-3731, BT-3733, BT-3736, and BT-3737. *O. taeniata* Link, 1807. Thailand (Phuket): BT-0171, BT-1293, BT-1294, BT-1295, and BT-1298. *O. tesselata* Lamarck, 1811. Philippines (Sulu): BT-4508, BT-4509, BT-4510, BT-4511, and BT-4512. *O. tricolor* Lamarck, 1811. Indonesia: DG-L15/10 (Flores, Awolong); DG-5326/14 (Bali); JS-026 and JS-027 (Java, Carita); BT-5015 (Tanimbar). *O. undatella* Lamarck, 1811. Ecuador (San Pedro): BT-2681. Mexico (Colima): BT-0331 and BT-0332. Panama (Venado Is.): BT-1665 and BT-1666. *O. vidua* Röding, 1798. Indonesia (Bali): BT-0601. Vanuatu: BT-0610 (Port Vila); BT-3312, BT-3313, and BT-3314 (no loc.). *O. williamsi* Melvill & Standen, 1897. Marshall Is. (Kwajalein): BT-2815, BT-2817, BT-2818, BT-2819, and BT-2820.

Genus *Olivancillaria*

O. contortuplicata Reeve, 1850. Uruguay (La Coronilla): BT-1013, BT-1089, BT-1091, BT-5901. *O. urceus* Röding, 1798. Brasil: BT-1073 (Sao Sebastiao, Praia do Paulista); BT-1079 and BT-1082 (Cabo Frio); BT-5867 (Rio de Janeiro). *O. uretai* Klappenbach, 1965. Argentina (Monte Hermoso): BT-2877, BT-2878, BT-2880, and BT-2881. *O. vesica vesica* Gmelin, 1791. Brasil (off Rio de Janeiro): BT-1064, BT-1065, BT-1066, BT-1069, and BT-1070.

Subfamily Olivellinae

Genus *Olivella s.l.*

O. anazora Duclos, 1835. Mexico (Manzanillo): BT-5880 and BT-5881. *O. gracilis* Broderip & Sowerby, 1829. Mexico (Nayarit): BT-5872, BT-5873, BT-5874, and BT-5875. *O. japonica* Pilsbry, 1895. Japan (off Mie Prefecture): BT-5885 and BT-5886. *O. pulchella* Duclos, 1835. Gambia (Cape St. Mary): BT-1716. Senegal (off Joal): BT-5878 and BT-5879. *O. volutella* Lamarck, 1811. Mexico (Manzanillo): BT-0449. Panama (Pedro Gonzales Is.): BT-0641, BT-5876, and BT-5877. *O. zanoeta* Duclos, 1835. Mexico (Manzanillo): BT-5887, BT-5888, and BT-5889. *O. zonalis* Lamarck, 1811. Panama (Isla del Rey): BT-0650 and BT-0652.

Subfamily Ancillinae

Ancilla (*Sparellina*) *acuminata* Sowerby, 1859. Somalia (no loc.): BT-1119, BT-1120, and BT-1121. *Ancilla* (*Sparellina*) *ampla* Gmelin, 1791. India (off Madras, 10 fms.): BT-0527, BT-5925, and BT-5926. *Baryspira australis* Sowerby, 1830. New Zealand (no loc.): BT-2897, BT-2898, and BT-5902. *Ancillus buccinoides* Lamarck, 1803. (Fossil, Lutetian). France (Champagne, Damery): BT-5913, BT-5915, and BT-5919. *Ancillarina canalifera* Lamarck, 1802. (Fossil, Lutetian). France (Champagne, Damery): BT-1208, BT-5903, and BT-5904. *Ancilla* (*Sparella*) *castanea* Sowerby, 1830. Saudi Arabia (Ras Tamura): BT-1133 and BT-1135. *Ancillista cingulata* Sowerby, 1830. W. Australia (Onslow): BT-1646, BT-3230, BT-3231, and BT-3232. *Ancilla cinnamomea* Lamarck, 1801. India (Cuddalore): BT-1127, BT-1128, BT-1129, and BT-1130. *Baryspira depressa* Sowerby, 1859. New Zealand (North Is., Waiki Beach): BT-2405, BT-2406, and BT-2407. *Amalda* (*?*) *dimidiata* Sowerby, 1850. This is the species illustrated pl.38, fig. 491 in Rios (1985). Brasil: BT-1049, BT-1050, and BT-1051 (off Itaipu, Rio de Janeiro); BT-5865 (off Santana, Rio). *Alocospira* (*?*) *edithae* Pritchard & Gatliff, 1898. S. Australia (Coffin Bay): BT-1812, BT-1814, and BT-5920. *Eburna glabrata* L., 1758. Venezuela (no loc.): BT-0988, BT-5558, BT-5860, and BT-5864. *Eburna lienardi* Bernardi, 1821. Brasil (Ceara, Acaraù): BT-0991, BT-0992, BT-0993, BT-0996, and BT-0997. *Ancilla* (*Sparellina*) *lineolata* A. Adams, 1853. Israel (Eilat): BT-1143, BT-1144, and BT-1145. *Alocospira* (*s.l.*) *marginata* Lamarck, 1810. Australia (Yorke Peninsula): BT-3274 and BT-3275; Tasmania (Ulverstone): BT-3261. *Ancilla* (*Hesperancilla*) *matthewsi* Burch & Burch, 1967. Brasil: BT-3497 and BT-3498 (Ceara, Fortaleza); BT-3499 (off Natal). *Alocospira* (*s.l.*) *monolifera* Reeve, 1864. W. Australia: BT-1045 (Albany); BT-1047 (Busselton); BT-3269 and BT-3272 (Margaret River). *Ancillista muscae* Pilsbry, 1826. W. Australia: BT-1051 (Exmouth); BT-1116 (no loc.); BT-3228 and BT-3229 (Onslow). *Gracilispira novaezelandiae* Sowerby, 1859. New Zealand (Mayor Is., 80 fms.): BT-2402, BT-2402a, and BT-2402b. *Ancilla* (*Sparellina*) *ovalis* Sowerby, 1859. Kuwait (Fintas): BT-5921, BT-5922, and BT-5924. *Ancillus olivula* Lamarck, 1803. (Fossil, Lutetian). France (Champagne, Damery): BT-5905, BT-5907, BT-5909, and BT-5910. *Alocospira* (*s.l.*) *rosea* Macpherson, 1951. Australia (Queensland, off Bushy Is.): BT-1801, BT-1802, and BT-1804. *Ancilla* (*Sparella*) *sarda* Reeve, 1864. Tanzania (Zanzibar): BT-1705, BT-1706, and BT-1707. *Amalda tankervillii* Swainson, 1825. Venezuela (no loc.): BT-2319, BT-2320, BT-5890, and BT-5891. *Ancillista velesiana* Iredale, 1936. Australia: BT-1669 (N.S.W., Tweed

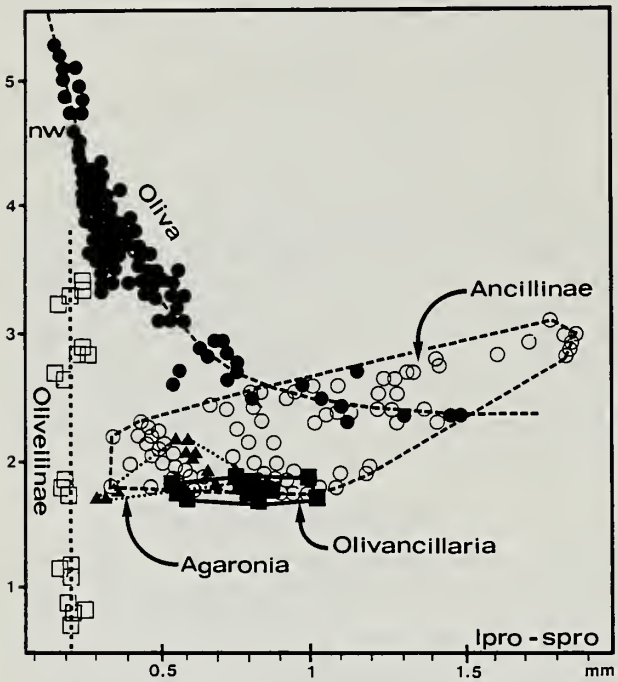

Figure 2

Family Olividae. Eighty-seven taxa. Scatter diagram of **nw** versus (**lpro** − **spro**).

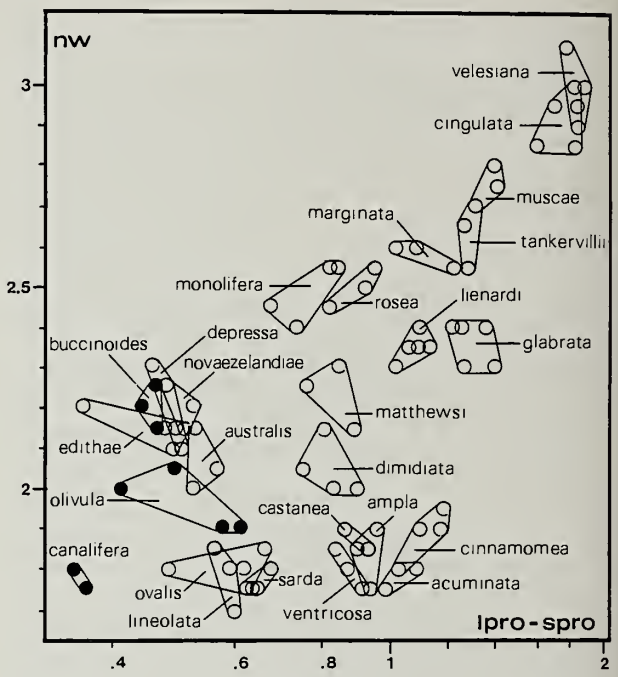

Figure 3

Subfamily Ancillinae. Scatter diagram of **nw** versus (**lpro** − **spro**). Grouping by species. Minimum convex polygons. Black circles: fossil species.

Heads); BT-3224 (no loc.); BT-5868 and BT-5869 (Queensland, Moreton Bay). *Ancilla* (*Sparella*) *ventricosa* Lamarck, 1811. SOMALIA (no loc.): BT-1122, BT-1124, and BT-1125.

RESULTS AND INTERPRETATION

Figure 2 shows the distribution of all observed points in a scatter diagram of **nw** versus (**lpro** − **spro**). This would show correlations between the number of whorls of the protoconch and the rate of lateral expansion of its spiral. It will be noted that the distribution of *Oliva* (black circles) is not at all random: all specimens fall on a smooth, regular curve, as if obeying precise construction rules. Only a part of this curve overlaps the somewhat looser area of distribution of the subfamily Ancillinae (white circles).

Too few species of the subfamily Olivellinae and the genera *Agaronia* and *Olivancillaria* are represented here to secure firm conclusions. These groups will not be discussed any further but it will nevertheless be noted that the species of Olivellinae examined so far (open squares) have a quite distinctive distribution and fall approximately into a straight line, with little or no variation in (**lpro** − **spro**). *Agaronia* (black triangles) and *Olivancillaria* (black squares) are well grouped, overlapping each other as well as the margin of the Ancillinae (in the region of the genus *Ancilla, cf.* Figure 4) but quite separated from the Olivellinae and the genus *Oliva*. The subfamily Ancillinae and the genus *Oliva* will be examined separately in more detail hereunder.

Figure 3 shows the distribution observed for the subfamily Ancillinae in a scatter diagram of **nw** versus (**lpro** − **spro**). It will allow the identification of species in Figures 4 and 5. One can observe that species are very well grouped: the usefulness of protoconch measurements for species recognition and separation, already shown for *Oliva* (TURSCH & GERMAIN [1985]; see also Figures 6 and 7 in this paper) can thus be extended to Ancillinae.

Figure 4 also shows the distribution observed for the subfamily Ancillinae in a scatter diagram of **nw** versus (**lpro** − **spro**). It is on the same scale as Figure 3, on which species can be identified individually. One can notice that the species are not distributed at random and that the distribution reflects supraspecific groupings. One is tempted to interpret this graph in terms of phylogeny, as the distribution fans out from the more primitive, fossil species (black circles) in the lower left corner to the most advanced *Ancillista* in the opposite corner.

According to Dr. R. N. Kilburn (in litt.), "*Amalda*" *muscae* is in fact an *Ancillista* (fragile shell, large, bifid foot—an adaptation for swimming—and broad rachidian plate). Its position on the graph (see Figure 3) is thus quite logical.

It will be noted that *Ancilla matthewsi* is found to be well separated from the other *Ancilla*. Other important differences (unique, crenulated ancillid groove and atypical radula) have been noted for this shell by KILBURN (1981) who concluded (p. 357): "The possibility exists . . . that *matthewsi* is actually an offshoot of an *Amalda* or *Eburna* lineage" and created the subgenus *Hesperancilla* Kilburn, 1981, to accommodate that species. Dr. Kilburn recently wrote to me that it might be an idea to use *Hesperancilla*

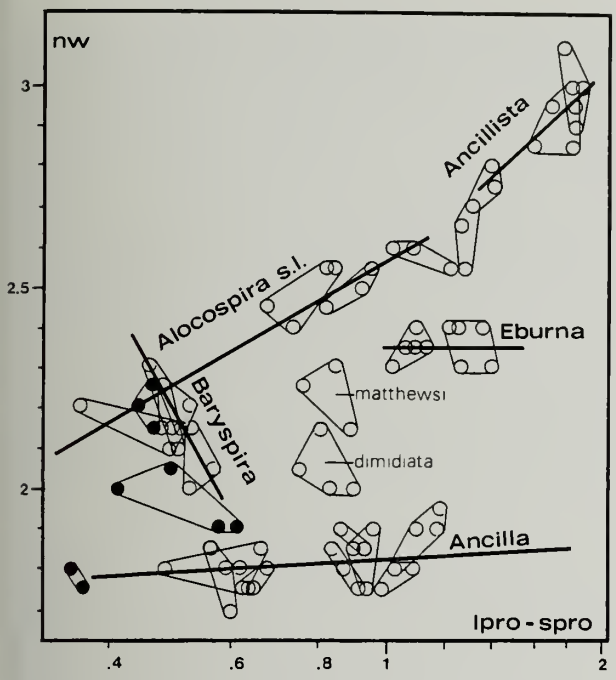

Figure 4

Subfamily Ancillinae. Scatter diagram of **nw** versus (**lpro** − **spro**). Grouping by supraspecific taxa (for species identification, see Figure 3). Minimum convex polygons. Black circles: fossil species.

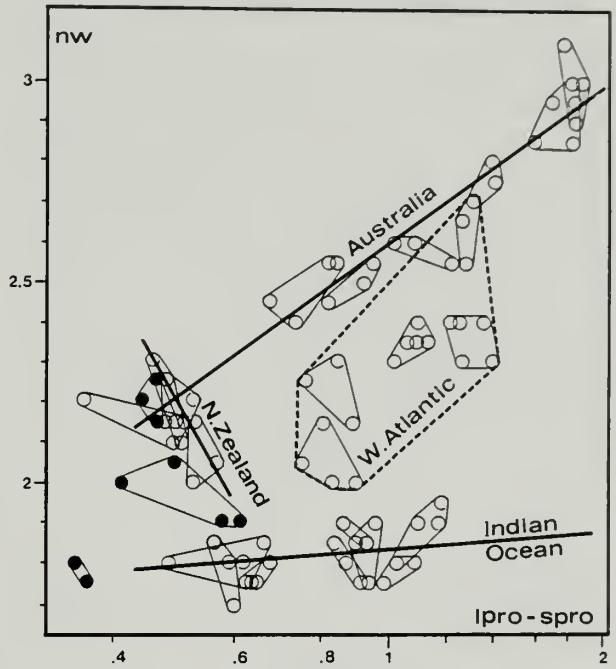

Figure 5

Subfamily Ancillinae. Scatter diagram of **nw** versus (**lpro** − **spro**). Grouping by geographical distribution (for species identification, see Figure 3). Minimum convex polygons. Black circles: fossil species.

as a full genus.The generic position of *dimidiata* is still not clearly established. I cannot comment yet on its position on the graph.

Figure 5 shows the same data, on the same scale, but interpreted in terms of zoogeography. The coherent patterns that are observed are not surprising: for animals having a direct development (with reduced larval dispersal) one would expect related species to occur in the same or neighboring regions.

Figure 6 shows that when represented in the system of axes **nw** and **1/(lpro − spro)** all specimens of *Oliva* are distributed along a nearly straight line. It will be noted that all 35 Indo-Pacific species examined (open squares) are closely grouped in the central part of the graph, in a range of values presumably close to the plesiomorphic (primitive) characters of the group. American and Atlantic species (black squares) are mostly found outside this zone (with the exception of *O. sayana* and *O. porphyria*).

Figure 7 is an enlargement of the "Indo-Pacific zone" of Figure 6. For the sake of clarity only 29 species have been represented. The missing species occur in the same general region as *Oliva caldania*. Here again it can be seen that intraspecific grouping is quite compact: most pairs of taxa can be unambiguously separated on the basis of only two protoconch characters.

DISCUSSION

From the data above, one can hardly escape the conclusion that protoconch measurements are meaningful at the su-

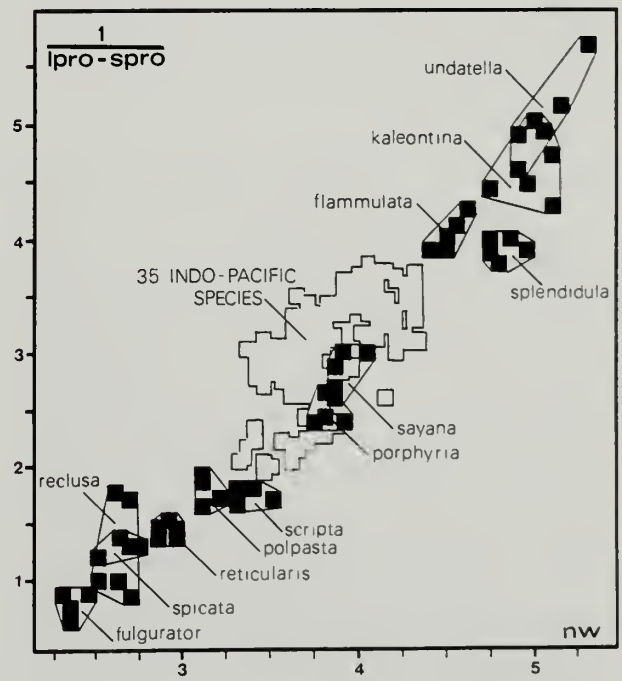

Figure 6

Genus *Oliva*. Scatter diagram of **1/(lpro − spro)** versus **nw**. American and Atlantic species: black squares (minimum convex polygons). Indo-Pacific species: white squares (detailed in Figure 7).

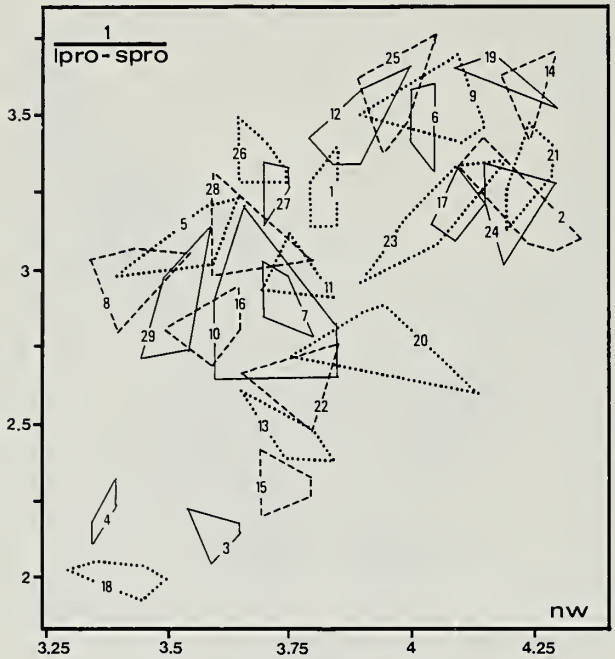

Figure 7

Genus *Oliva*: Indo-Pacific species (see text). Scatter diagram of **1/(lpro − spro)** versus **nw**. Minimum convex polygons. 1: *O. amethystina*. 2: *O. arctata*. 3: *O. australis*. 4: *O. buelowi*. 5: *O. bulbosa*. 6: *O. bulbiformis*. 7: *O. caerulea*. 8: *O. caldania*. 9: *O. carneola*. 10: *O. caroliniana*. 11: *O. concinna*. 12: *O. dubia*. 13: *O. hirasei*. 14: *O. lacanientai*. 15: *O. lenhilli*. 16: *O. lignaria*. 17: *O. mantichora*. 18: *O. miniacea*. 19: *O. neostina*. 20: *O. ornata*. 21: *O. paxillus*. 22: *O. rufofulgurata*. 23: *O. rufula*. 24: *O. semmelinki*. 25: *O. sidelia*. 26: *O. taeniata*. 27: *O. tesselata*. 28: *O. tricolor*. 29: *O. williamsi*.

praspecific level. There is a good agreement between the observed clusters of protoconch measurements and the commonly accepted supraspecific groupings (established on completely independent grounds).

There is no real contradiction between this conclusion and the statement of BOUCHET (1987:78; see also p. 109): "le mode de développement larvaire, et sa transcription dans la morphologie de la protoconque, ne traduit pas des liens de parenté et n'a aucune valeur taxonomique au niveau supraspécifique. . . ." The author has carefully defined "mode de développement" as being the planctotrophic or non-planctotrophic modes of development and his negative conclusions are restricted to planctotrophic species, as clearly stated (p. 108): "En conclusion, les protoconques planctotrophiques ne constituent pas (pas encore ?) un outil classificatoire aux rangs supraspécifiques." This conclusion obviously does not apply to Olividae as these have a non-planctotrophic (intracapsular) mode of development (PETUCH & SARGENT, 1986) like the related family Volutidae (BOUCHET, 1987).

The spread of the different species in the graphs does not represent the real variability range, the randomly selected samples being far too small. In the cases for which large samples have been examined (see for instance TURSCH *et al.*, 1986b) intraspecific variation remains small.

The striking regularities observed for the distributions of protoconch measurements in *Oliva* and *Olivella* do not necessarily have to be explained by direct adaptation; they might well reflect an architectural constraint in the building of these particular types of protoconchs (see GOULD & LEWONTIN, 1978).

It is very unlikely that protoconch shape and size would be dependent on local ecological factors alone. For instance, *Oliva spicata* and *O. kaleontina* have very dissimilar protoconchs and yet can be found side by side in the Panamic region. An interpretation in terms of phylogeny seems more plausible.

I do not advocate here a supraspecific classification of Olividae based upon protoconch characters alone. Furthermore, great caution should be exerted in the interpretation of the data hereabove because coincidence of points in the graphs does not necessarily imply identity of protoconch types. Proper representation of protoconch morphological trends requires a multidimensional space (with as many reference axes as there are characters to be taken into account). In bi-dimensional graphs such as those presented here, constellations of neighboring points (just like constellations of stars) can include objects separated by large distances along another dimension. It should be remembered that **nw**, **lpro** and **spro** do not determine the shape or the size of the protoconch. As an example, the protoconchs of *Eburna glabrata* and of *Oliva fulgurator* have similar values for **nw** and (**lpro** − **spro**) but are very dissimilar in other aspects.

Much additional work is required for the exploration of the 10 other protoconch variables defined in TURSCH & GERMAIN, (1985, 1986a). Research along these lines is being actively pursued in this laboratory.

ACKNOWLEDGMENTS

This work could not be done without the help of L. Germain: most computer programs utilized here are largely his work. Much computer help also came from O. Vronen. I thank Dr. H. Coomans (Instituut voor Taxonomische Zoölogie, Zoölogische Museum, Amsterdam), A. Bossuyt (Wervik), Dr. D. Greifeneder (Schwenningen), R. Martin (Cebu), F. Nolf (Ostende), and J. Senders (Brussels) for loans and gifts of specimens.

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LITERATURE CITED

BOUCHET, P. 1987. La protoconque des gastéropodes. Thèse de doctorat d'Etat, Museum National d'Histoire Naturelle and Université Pierre et Marie Curie, Paris. 181 pp.

GOULD, S. J. & R. C. LEWONTIN. 1978. The spandrels of San

Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. Roy. Soc. Lond. 205:581–598.

Kilburn, R. N. 1977. Description of new species of *Amalda* and *Chylotygma* (Gastropoda: Olividae: Ancillinae) with a note on the systematics of *Amalda, Ancillus* and *Ancillista*. Ann. Natal Mus. 23(1):13–21.

Kilburn, R. N. 1981. Revision of the genus *Ancilla* Lamarck, 1799. Ann. Natal Mus. 24(2):349–463.

López, A., M. Montoya & J. López. 1988. A review of the genus *Agaronia* (Olividae) in the Panamic Province and the description of two new species from Nicaragua. Veliger, 30(3):295–304.

Petuch, E. J. & D. M. Sargent. 1986. Atlas of the living olive shells of the world. Coastal Education and Research Foundation: Charlottesville, Virginia. 253 pp.

Rios, E. C. 1985. Seashells of Brasil. Fundaçao Universidade do Rio Grande: Rio Grande, R.S., Brasil. 309 pp., 102 pl.

Tursch, B. & L. Germain. 1985. Studies on Olividae. I. A morphometric approach to the *Oliva* problem. Indo-Malayan Zoology 2:331–352.

Tursch, B. & L. Germain. 1986a. Studies on Olividae. II. Further protoconch morphometrical data for *Oliva* taxonomy. APEX (Informations scientifiques de la Société Belge de Malacologie) 1(2):39–45.

Tursch, B. & L. Germain. 1986b. Studies on Olividae. V. Five additional protoconch characters for *Oliva* taxonomy. APEX 2(3–4):59–68.

Tursch, B., L. Germain & D. Greifeneder. 1986a. Studies on Olividae. III. Description of a novel subspecies: *Oliva bulowi phuketensis*. APEX 1(3):71–87.

Tursch, B., L. Germain & D. Greifeneder. 1986b. Studies on Olividae. IV. *Oliva annulata* Gmelin, 1791 (of authors): a confusion of species. Indo-Malayan Zoology 3:189–216.

Zeigler, R. F. & H. C. Porreca. 1969. Olive shells of the world. Rochester Polychrome Press: Rochester, New York. 96 pp.

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A New Subgenus of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae) with the Description of a New Species from San Bernardino County, California

by

RICHARD L. REEDER

Faculty of Biological Science, University of Tulsa, Tulsa, Oklahoma 74104, U.S.A.

AND

BARRY ROTH

Department of Invertebrate Zoology, Santa Barbara Museum of Natural History, 2559 Puesta Del Sol Road, Santa Barbara, California 93105, U.S.A.

Abstract. ***Coyote,*** a new subgenus of *Helminthoglypta,* is described; it is characterized by a prominent bulge at the anterior end of the upper penial chamber and a papillose shell. It includes the so-called "Mojave Desert Series" and the polytypic *Helminthoglypta petricola* from the San Bernardino, San Gabriel, and Santa Ana mountains, California. The type species, *Helminthoglypta* (***Coyote***) ***taylori***, sp. nov., is described from near the headwaters of the Mojave River, San Bernardino County, California.

INTRODUCTION

This paper continues a series of studies of new helminthoglyptid taxa from southern California based in part on land snails originally collected by the late Wendell O. Gregg (1898–1979). The other papers in the series include Gregg & Miller (1976), Miller (1985), Reeder (1986), Reeder & Miller (1986a, b, 1987, 1988), Roth (1987a), and Roth & Hochberg (1988, this issue). As a result of earlier studies, Gregg and Walter B. Miller determined that the subgenus *Charodotes* Pilsbry, 1939, of the genus *Helminthoglypta* Ancey, 1887, was based on erroneous information about the structure of the upper chamber of the penis. Miller (1981, 1985) synonymized *Charodotes* with the nominate subgenus. Gregg and Miller further determined that there were at least two distinct groups of species in *Helminthoglypta* (in addition to the nominate subgenus) that deserved subgeneric recognition. The first of these was described as *Rothelix* Miller, 1985; it is characterized by a relatively short and narrow upper penial chamber; a large, sausage-shaped, lower chamber with a post-medial constriction; and a vagina that opens into the atrial sac near its posterior end.

The second group consists of species united in the possession of a distinctive, prominent bulge at the anterior end of the upper, double-tubed chamber of the penis. This group includes the "Mojave Desert Series" of Pilsbry (1939), the polytypic *Helminthoglypta petricola* (Berry, 1916) of the San Bernardino, San Gabriel, and Santa Ana mountains, and a number of other species from ranges peripheral to the Mojave Desert.

One such peripheral species was discovered by Dwight W. Taylor and Gregg in April 1950, along the headwaters of the Mojave River near the town of Cedar Springs in the San Bernardino Mountains. Miller and Gregg obtained additional material in 1963 from a locality which, along with the town of Cedar Springs, was later inundated by the waters of Silverwood Lake, impounded by Cedar Springs Dam. Fortunately, field investigations by Miller and Roth in early 1986 revealed that the species continues to thrive in a limited area below Cedar Springs Dam, and

the species is described herein, along with the subgenus to which it belongs.

Terminology for the elements of the reproductive system follows that of MILLER (1985), except that what MILLER (1985) referred to as the upper and lower "parts" of the penis are here called the upper and lower chambers of the penis.

SYSTEMATICS

Family HELMINTHOGLYPTIDAE Pilsbry, 1939

Helminthoglypta Ancey, 1887

Type species: *Helix tudiculata* A. Binney, 1843, by original designation.

Coyote Reeder & Roth, subgen. nov.

Type species: *Helminthoglypta* (***Coyote***) ***taylori*** Reeder & Roth, sp. nov.

Diagnosis: Shell medium-sized to small for the genus, depressed, umbilicate, with varying degrees of papillose sculpture. Reproductive system distinguished by a prominent bulge at the anterior end of the upper, double-tubed chamber of the penis.

All members of ***Coyote*** exhibit a prominent swelling at the anterior end of the upper, double-tubed chamber of the penis where it joins the lower, saccular chamber (Figure 1). This bulge is caused by a pronounced thickening of the walls of the inner tube of the penis, usually accompanied by enlarged, glandular pilasters along the widening lumen. The bulge projects permanently into the lower chamber, forming a short penis-papilla. While some specimens of *Helminthoglypta, sensu stricto,* occasionally exhibit a small penis-papilla in the lower part of the penis as a result of the process used in preparing anatomical whole mounts, they do not have the characteristic thickened walls of the anterior part of the inner tube shown by the species of ***Coyote***.

In addition to the distinctive anatomy, all species of ***Coyote*** have papillose sculpture, ranging from a dense, overall papillation (*e.g., Helminthoglypta mohaveana* Berry, 1927), to the regular, discrete tubercles of *Helminthoglypta petricola*. The malleated sculpture of *Helminthoglypta tudiculata, Helminthoglypta fairbanski* Reeder & Miller, 1986, and others of that group does not appear in species of ***Coyote***. The clothlike sculpture of *Helminthoglypta nickliniana* (Lea, 1838) and its relatives is also absent from ***Coyote***. Although some incised spiral lines occur in *H. petricola,* no species of ***Coyote*** exhibits the prominent grooves found in *Helminthoglypta fieldi* Pilsbry, 1930, *Helminthoglypta ayresiana* (Newcomb, 1861), and some other members of the *Helminthoglypta traskii* (Newcomb, 1861) group.

Based on an examination of their reproductive systems, the following additional species and subspecies are assigned to this subgenus:

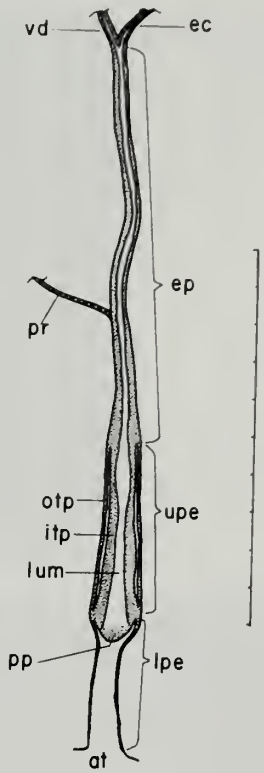

Figure 1

Helminthoglypta (***Coyote***) ***taylori*** Reeder & Roth, sp. nov., holotype SBMNH 34945, penis and epiphallus; drawn from projection of stained whole mount. Scale line = 10 mm. Abbreviations: at, atrium; ec, epiphallic caecum; ep, epiphallus; itp, inner tube of penis; lpe, lower chamber of penis; lum, lumen of penis; otp, outer tube of penis; pp, penis-papilla; pr, penial retractor muscle; upe, upper chamber of penis; vd, vas deferens.

Helminthoglypta fisheri (Bartsch, 1904)
H. petricola (Berry, 1916)
  H. p. zechae (Pilsbry, 1916)
  H. p. sangabrielis (Berry, 1920)
  H. p. orotes (Berry, 1920)
H. graniticola Berry, 1926
H. mohaveana Berry, 1927
H. crotalina Berry, 1928
H. jaegeri Berry, 1928
H. fontiphila Gregg, 1931
H. greggi Willett, 1931
H. isabella Berry, 1938
H. micrometalleoides Miller, 1973
H. concolor Roth & Hochberg, 1988.

The reproductive anatomy of *Helminthoglypta caruthersi* Willett, 1934, is unknown and the species has not been collected since its original discovery. However, based on shell characters and geography, it also probably belongs to the subgenus ***Coyote***. In addition, the middle Miocene (Barstovian) *Helminthoglypta alfi* Taylor, 1954, which

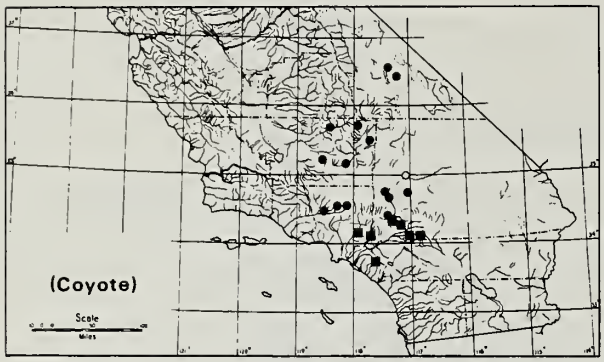

Figure 2

Map of southern California showing distribution of ***Coyote***, subgen. nov. Solid circles, species of "Mojave Desert Series" of PILSBRY (1939); open circle, *Helminthoglypta alfi*, Barstow Formation (Miocene); solid squares, *Helminthoglypta petricola*.

TAYLOR (1954) assigned to the Mojave Desert Series, probably belongs to this subgenus.

Helminthoglypta venturensis (Bartsch, 1916), described from Ventura County but never subsequently recognized, may be another member of ***Coyote***. The holotype is sculptured similarly to *H.* ***taylori*** and *H. fontiphila. Helminthoglypta venturensis* was originally described as a subspecies of *Helminthoglypta* (*Rothelix*) *cuyamacensis* (Pilsbry, 1895), but until living specimens are found and dissected, it cannot be firmly allocated.

Figure 2 depicts the distribution of the subgenus ***Coyote***. The development of the Mojave Desert Series suggests an ancestral distribution along the course of the Mojave River and its tributaries prior to the rise of the Peninsular Ranges and Transverse Ranges to their present elevation and the (late Pliocene or early Pleistocene) onset of extreme aridity in the region. During much of this time, in the absence of a mountain barrier to the west, the major Mojave drainage may have been southwestward toward the Pacific coast, rather than eastward toward the Colorado River.

Etymology: ***Coyote***, from the Nahuatl *coyotl*: the prairie wolf (*Canis latrans*), a figure in indigenous American mythology.

Helminthoglypta (***Coyote***) ***taylori***
Reeder & Roth, sp. nov.

(Figures 1, 3–5)

Diagnosis: Shell of medium size for the genus, coarsely, densely papillose, above and below; papillae extending all the way to the peristome and into the umbilicus, confluent behind lip. Reproductive anatomy typical of subgenus ***Coyote***, with prominent swelling of anterior portion of upper penial chamber forming a penis-papilla.

Description of shell of holotype: Shell (Figures 3–5) of medium size for the genus, thin, translucent, matte to silky, depressed, umbilicate, umbilicus contained 11.0 times in major diameter. Spire very low-conic, whorl profile moderately convex, roundly shouldered; suture strongly impressed. Embryonic whorls 1.6, not strongly differentiated from first teleoconch whorl; initial half whorl smooth, thereafter with radiating rows of round to ovate papillae, grading after 0.25 whorl into irregular, granulose, predominantly radial wrinkling. Early teleoconch whorls with low, retractive growth rugae, strongest below suture, extremely fine radial wrinkling overall, and (most noticeably from third whorl on) minute, spirally elongated papillae in curved, obliquely descending rows. Papillae becoming larger and more irregular on subsequent whorls, running together in some places, especially on body whorl behind aperture; most papillae with depressed rim setting them off from wrinkled background surface. Papillae prominent on body whorl, continuing over base into umbilicus, sparser and less prominent on periphery and base of last growth increment. Base inflated, tumid around umbilicus, surface between papillae smooth. Body whorl rapidly descending, not constricted behind lip. Aperture subcircular except for interruption by parietal wall, oblique, plane of peristome at angle of 45° to vertical; lip slightly thickened and turned outward, most strongly reflected at base. Upper limb of peristome produced and slightly downturned; outer lip weakly sinuous. Inner lip encroaching slightly on umbilicus. Parietal callus thin, with irregular granulation; papillae of penultimate whorl showing through. Shell pale pinkish tan under a yellowish-brown periostracum; with a 1-mm wide russet spiral band on shoulder (prolonging trajectory of suture) with paler zones of equal width on either side of band.

Dimensions of holotype: Diameter (exclusive of expanded lip) 20.9 mm, height 12.0 mm, diameter of umbilicus 1.9 mm, 5.3 whorls.

Reproductive anatomy of holotype: The genitalia are, in general, typical of the genus with a long, spacious atrial sac having a small dart sac at its proximal end and having two mucous glands with mucous bulbs, the ducts of which unite before entering the proximal end of the atrial sac. The vagina opens into the distal end of the atrial sac. The spermatheca is spherical with a long duct having a spermathecal diverticulum diverging at a point approximately midway along the length of the duct. The penis (Figure 1) has upper and lower divisions, the lower chamber being a saccular, single-walled organ. The upper chamber is double-tubed, with the walls of the inner tube expanding abruptly at the anterior end to form a penis-papilla which projects into the lower chamber. The epiphallus is of moderate length with a short epiphallic caecum. The penial retractor muscle attaches to the epiphallus. Measurements of structures are as follows: penis 6.7 mm, epiphallus 8.9 mm, epiphallic caecum 18.2 mm, spermathecal duct 10.7 mm, spermathecal diverticulum 18.4 mm, vagina 6.0 mm.

Disposition of types: Holotype (shell and whole mount of reproductive system): Santa Barbara Museum of Nat-

Explanation of Figures 3 to 5

Figures 3–5. *Helminthoglypta* (***Coyote***) ***taylori***, sp. nov., holotype SBMNH 34945, shell; top, apertural, and basal views; diameter 20.9 mm.

ural History, SBMNH 34945. Paratypes (15 shells): SBMNH 34946; additional paratypes (shells) deposited in Academy of Natural Sciences of Philadelphia, Los Angeles County Museum of Natural History, U.S. National Museum of Natural History, and the private collections of W. B. Miller, R. L. Reeder, and B. Roth.

Type locality: California: San Bernardino County: bank of West Fork of Mojave River, at junction of Cedar Springs Road and Summit Valley Highway; elevation approximately 960 m (3150 ft); under cottonwood logs and decaying leaves. W. B. Miller coll., 9 May 1963.

Referred material: Additional specimens have been examined from the following localities (all, California: San Bernardino County). The collectors' original topographic measurements, usually expressed in miles and feet, have been preserved, with metric equivalents added. The first three locality descriptions probably refer to essentially the same site.

West Fork of Mojave River on road to Cedar Springs. W. O. Gregg and D. W. Taylor coll., 12 April 1950 (WBM). West bank of West Fork of Mojave River, north of bridge on Cedar Springs Road, elevation 3150 ft [960 m]. E. P. Chace and W. O. Gregg coll., 7 April 1956; W.

O. Gregg coll., 4 November 1958 (WBM). West branch of West Fork of Mojave River north of bridge on Cedar Springs Road, 11.1 mi [17.8 km] east of [former] U.S. Highway 66. W. O. Gregg coll., 2 June 1963 (WBM). Along West Fork of Mojave River, approximately 100 yards [90 m] north of Cedar Springs Dam, elevation 3100 ft [945 m], under cottonwood logs. W. B. Miller coll., 11 February 1986 (WBM). Along unnamed creek tributary to West Fork of Mojave River, just north of California Highway 173, east of spillway of Cedar Springs Dam, under sycamore and branches on ground. B. Roth coll., 24 April 1986 (BR).

Discussion: In the material at hand, adult shell diameter ranges from 16.4 to 22.8 mm (mean of 20 specimens including holotype, 19.4 mm); height 9.7 to 12.9 mm ($\bar{x}$ = 11.5 mm); number of whorls 5.0 to 5.6 ($\bar{x}$ = 5.3). Diameter of umbilicus ranges from 1.4 to 2.5 mm ($\bar{x}$ = 1.9 mm), contained 8.0 to 11.7 times in major diameter of shell.

The spire ranges from nearly flat to low-conic. The number of embryonic whorls ranges from 1.6 to 1.75. There is minor variation in the strength and regularity of papillation, and many of the paratypes show traces of incised spiral lines, particularly on the shoulder of the body whorl. The major trend of the microscopic periostracal wrinkling is radial on early whorls but becomes spiral on later whorls.

The shallow S-curve of the outer lip (as seen in lateral view), convex above the periphery and concave below, is quite distinctive. On most specimens, the lip is very little thickened and expanded at maturity; however, on one paratype the lip is turned outward into a 0.75-mm flange, most strongly reflected at the base. Several specimens have an internal varix (*cf.* ROTH 1987b) 1–2 mm behind a strong growth rest line.

Helminthoglypta ***taylori*** is larger than most species of the Mojave Desert Series and much more narrowly umbilicate. For example, in *H. mohaveana* the umbilicus is contained in the major diameter about 6.6 times; in *H. isabella,* about 7.5 times; in *H. jaegeri,* about 6.4 times. *Helminthoglypta fontiphila* differs in its generally smaller size (diameter 15.7–16.7 mm) and its finer, closer, overall papillation; in many specimens of *H. fontiphila* the papillae bear periostracal setae.

Approximately 7 km upstream from the type locality of *Helminthoglypta* ***taylori***, a population of *H. petricola* occurs along the East Fork of the West Fork of the Mojave River, at an elevation of 1100 m in Miller Canyon (NW¼ SW¼ sec. 10, T. 2 N, R. 4 W, San Bernardino Base and Meridian). The spire is higher, the base more deeply rounded than in *H.* ***taylori***. The shell is glossy, with smaller papillae in oblique series, often confluent into neat, low ridges sloping obliquely downward in the direction of growth; the papillae become sparse in the umbilical area. Weakly incised spiral lines are present on the base. There are 1.8 embryonic whorls, and the early sculpture consists of a mixture of large and small granules. The suture is appressed, rather than strongly impressed as in *H.* ***taylori***.

Habitat: The dominant vegetation in the region is Juniper-Pinyon Woodland (KÜCHLER 1977), grading to Chaparral up the canyon of the West Fork. Below Cedar Springs Dam, *Helminthoglypta* ***taylori*** occurs in a sandy, riparian zone with Fremont Cottonwood (*Populus fremontii* Wats.), Western Sycamore (*Platanus racemosa* Nutt.), and willows (*Salix* spp.).

Etymology: This species is named for our colleague, Dwight W. Taylor, who, with W. O. Gregg, first discovered it along the headwaters of the Mojave River.

ACKNOWLEDGMENTS

We are indebted to the late Wendell O. Gregg for material used in this study and to our friend and colleague, Walter B. Miller, for providing specimens and notes, preparing the anatomical figure, and companionship in the field. We are grateful to Susan J. McKee for preparing photographs of the shell and for companionship in the field. We would also like to thank Diane M. Bohmhauer of the U.S. National Museum for the loan of comparative material. We also extend thanks to Barbara Barnard and Jan Bingham for clerical and other assistance.

LITERATURE CITED

GREGG, W. O. & W. B. MILLER. 1976. Two new species of *Helminthoglypta* (Mollusca: Pulmonata) from San Diego County, California. Bull. So. Calif. Acad. Sci. 75(1):10–16.

KÜCHLER, A. W. 1977. The map of the natural vegetation of California. Pp. 909–939, map. *In:* M. G. Barbour & J. Major (eds.), Terrestrial vegetation of California. John Wiley and Sons: New York.

MILLER, W. B. 1981. *Helminthoglypta reederi* spec. nov. (Gastropoda: Pulmonata: Helminthoglyptidae) from Baja California, Mexico. Veliger 24(1):46–48.

MILLER, W. B. 1985. A new subgenus of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae). Veliger 28(1):94–98.

PILSBRY, H. A. 1939. Land Mollusca of North America (north of Mexico). Acad. Natur. Sci. Philadelphia, Monogr. 3, 1(1): i–xviii, 1–573, i–ix.

REEDER, R. L. 1986. A new species of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae) from the Cuyamaca Mountains of southern California. Veliger 28(4):444–447.

REEDER, R. L. & W. B. MILLER. 1986a. A new species of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae) from San Diego County, California. Proc. Biol. Soc. Washington 99(1):137–139.

REEDER, R. L. & W. B. MILLER. 1986b. A description of a new *Helminthoglypta s.s.* (Gastropoda: Pulmonata: Helminthoglyptidae) from San Diego County, California. Veliger 29(1):129–131.

REEDER, R. L. & W. B. MILLER. 1987. A new *Helminthoglypta* (*Rothelix*) (Gastropoda: Pulmonata: Helminthoglyptidae) from southern California with comments on its probable

evolutionary relationships. The Southwestern Naturalist 32(2):261–265.

Reeder, R. L. & W. B. Miller. 1988. A new *Helminthoglypta* (*Rothelix*) (Gastropoda: Pulmonata: Helminthoglyptidae) from Warner Springs, San Diego County, California. Veliger 31(1/2):87–90.

Roth, B. 1987a. A new and polytypic species of *Helminthoglypta* (Gastropoda: Pulmonata) from the Transverse Ranges, California. Veliger 30(2):184–189.

Roth, B. 1987b. Structure of internal varices in the shell of *Micrarionta rufocincta* and other Helminthoglyptidae (Gastropoda: Pulmonata). Bull. So. Calif. Acad. Sci. 86(3):145–152.

Roth, B. & F. G. Hochberg, Jr. 1988. A new species of *Helminthoglypta* (*Coyote*) (Gastropoda: Pulmonata) from the Tehachapi Mountains, California. Veliger 31(3/4):258–261.

Taylor, D. W. 1954. Nonmarine mollusks from Barstow Formation of southern California. U.S. Geol. Surv. Prof. Paper 254-C:67–80, pl. 20.

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A New Species of *Helminthoglypta* (*Coyote*) (Gastropoda: Pulmonata) from the Tehachapi Mountains, California

by

BARRY ROTH AND F. G. HOCHBERG, JR.

Department of Invertebrate Zoology, Santa Barbara Museum of Natural History, Santa Barbara, California 93105, U.S.A.

Abstract. A new species of helminthoglyptid land snail, *Helminthoglypta* (*Coyote*) ***concolor***, is described from the upper part of Tejon Canyon, Tehachapi Mountains, Kern County, California. It is similar to *Helminthoglypta* (*Coyote*) *isabella* from the Kern River drainage, and is the second known species of the subgenus *Coyote* from the San Joaquin Valley watershed. Fossils of *Helminthoglypta* sp., *cf. H.* (*Coyote*) *graniticola,* occur in the Cable Formation, lakebed deposits of probable Pliocene age in the Tehachapi Valley, 16 km north of the known range of *H.* ***concolor***.

INTRODUCTION

Tejon Creek, Kern County, California, drains northwest from the Tehachapi Mountains into the San Joaquin Valley. In the 1950s and early 1960s, W. O. Gregg and W. B. Miller investigated the mollusks of the environs of Tejon Creek, finding three species of the land snail genus *Helminthoglypta,* one of them undescribed. In March 1987 the authors and W. B. Miller returned to the area to secure additional live material and add observations on distribution.

The vegetation of the Tejon Creek area is Blue Oak-Digger Pine Forest, grading upward into patches of Northern Jeffrey Pine Forest (KÜCHLER, 1977). Above approximately 1600 m elevation, White Fir, *Abies concolor* (Gord. & Glend.) Lindl., becomes a prominent component of the forest. Lower elevations are extensively overgrazed, and the principal snail cover is in Western Sycamore (*Platanus racemosa* Nutt.) and Fremont Cottonwood (*Populus fremontii* Wats.) deadfalls and debris piles close to Tejon Creek. Here were found *Helminthoglypta* (*Helminthoglypta*) *berryi* Hanna, 1916, and *Helminthoglypta* (*H.*) *avus* (Bartsch, 1916). In the zone of White Fir, a new species of the subgenus *Coyote,* described below, occurred sparingly under the bark of decaying fir deadfalls and in loose fir bark on the ground.

The following abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; BR, senior author's collection, San Francisco, California; CAS, California Academy of Sciences geology localities; LACM, Natural History Museum of Los Angeles County; SBMNH, Santa Barbara Museum of Natural History; USNM, U.S. National Museum of Natural History; WBM, collection of W. B. Miller, Tucson, Arizona.

SYSTEMATICS

Family HELMINTHOGLYPTIDAE Pilsbry, 1939

Helminthoglypta Ancey, 1887

Type species: *Helix tudiculata* A. Binney, 1843, by original designation.

Subgenus *Coyote* Reeder and Roth, 1988

Type species: *Helminthoglypta* (*Coyote*) *taylori* Reeder and Roth, 1988, by original designation.

Helminthoglypta (*Coyote*) ***concolor***
Roth & Hochberg, sp. nov.

(Figures 1–4)

Diagnosis: A medium-sized *Helminthoglypta* with depressed, thin, broadly umbilicate shell sculptured with closely spaced, anastomosing growth rugae and regular papillation; whorl diameter increasing rapidly; prominent bulge at anterior end of upper, double-tubed chamber of

Explanation of Figures 1 to 3

Helminthoglypta ***concolor*** Roth & Hochberg, shell; holotype SBMNH 34947, top, apertural, and basal views. Diameter 23.1 mm.

penis, caused by thickening of walls of inner penial tube; broad penis-papilla present.

Description of shell of holotype: Shell (Figures 1–3) large for the subgenus, thin, translucent, of silky luster, strongly depressed, broadly umbilicate, umbilicus contained 7.7 times in major diameter. Spire barely elevated, whorl profile weakly convex, suture distinctly impressed. Embryonic whorls 1.8, narrower than first neanic whorl; initial half whorl smooth, thereafter with radiating rows of round to ovate papillae, grading after 0.25 whorl into irregular radial wrinkles. Early neanic whorls with low, narrow, closely spaced growth rugae, extremely fine radial wrinkling overall, and (most noticeably from third whorl on) minute, round, discrete papillae in obliquely descending rows. Growth rugae strong on later whorls, frequently anastomosing. Papillae becoming larger on subsequent whorls and elongated in direction of growth, many with depressed rim setting them off from wrinkled or pebbly background surface; an extra scattering of smaller papillae present just outboard of suture on later whorls. Papillae prominent on body whorl, continuing less densely over base into umbilicus. Base moderately inflated, tumid around umbilicus, surface between papillae smooth. Body whorl rapidly expanding, gently descending, not constricted behind lip. Aperture broadly auricular, oblique, plane of peristome at angle of 45° to vertical; lip weakly turned outward, not thickened, scarcely reflected except at columellar insertion. Upper limb of peristome produced and slightly downturned. Inner lip barely encroaching on umbilicus. Parietal callus thin, glossy, with papillae of parietal wall showing through. Shell pinkish tan under a yellowish-brown periostracum; with a 1.5-mm-wide russet spiral band on shoulder (prolonging trajectory of suture) with traces of narrower pale zones on either side of band. Diameter (exclusive of expanded lip) 23.1 mm, height 12.0 mm, width of umbilicus 3.0 mm, whorls 5.25.

Type material: Holotype: Santa Barbara Museum of Natural History, SBMNH 34947 (shell), California: Kern County: Tejon Canyon, 16.5 km (10.3 road mi) E of cemetery [NE¼ sec. 30, T. 11 N, R. 15 W, San Bernardino Base and Meridian], elevation approximately 1600 m (5300 ft); in White Fir deadfalls. W. B. Miller, F. G. Hochberg, B. Roth coll., 7 March 1987.

Paratypes: SBMNH 34948 (7 shells); SBMNH 34950 (1 shell, stained whole mount of reproductive system, and whole mount of mantle), from same locality as holotype. Additional paratypes deposited in ANSP, BR, LACM, USNM, and WBM.

Referred material (all, California: Kern County)**:** South of sawmill at head of Tejon Canyon, elev. 1600 m [5300 ft], W. O. Gregg, W. B. Miller coll., 3–4 May 1958 (LACM 114645). Headwaters of Tejon Creek at sawmill 29.8 km [18.6 mi] up Tejon Canyon from Tejon Ranch headquarters, W. B. Miller coll., 3 May 1958 (WBM 2942).

Soft anatomy: The mantle over the lung is clear buff, heavily (50–60%) maculated with black. The reproductive system (Figure 4) is typical of the subgenus *Coyote* in having a prominent swelling at the anterior end of the upper, double-tubed chamber of the penis where it joins the lower, saccular chamber. This swelling is caused by a pronounced thickening of the walls of the inner penial tube. A short, broad penis-papilla projects into the lower, saccular chamber. Three low pilasters run the length of the lower chamber.

The epiphallic caecum is notably long, approximately 1.5 times the length of penis plus epiphallus. The penial retractor muscle inserts a short distance anterior to the summit of a crook in the epiphallus.

The atrial sac is longer than the vagina and relatively slender; it bears a rather small, ovate dart sac at its proximal end. The mucus gland bulbs are short and broad, joined by a slender common duct that inserts at the summit of the atrial sac. The spermathecal duct bears a very long diverticulum, approximately twice as long as the part of the spermathecal duct above the origin of the diverticulum.

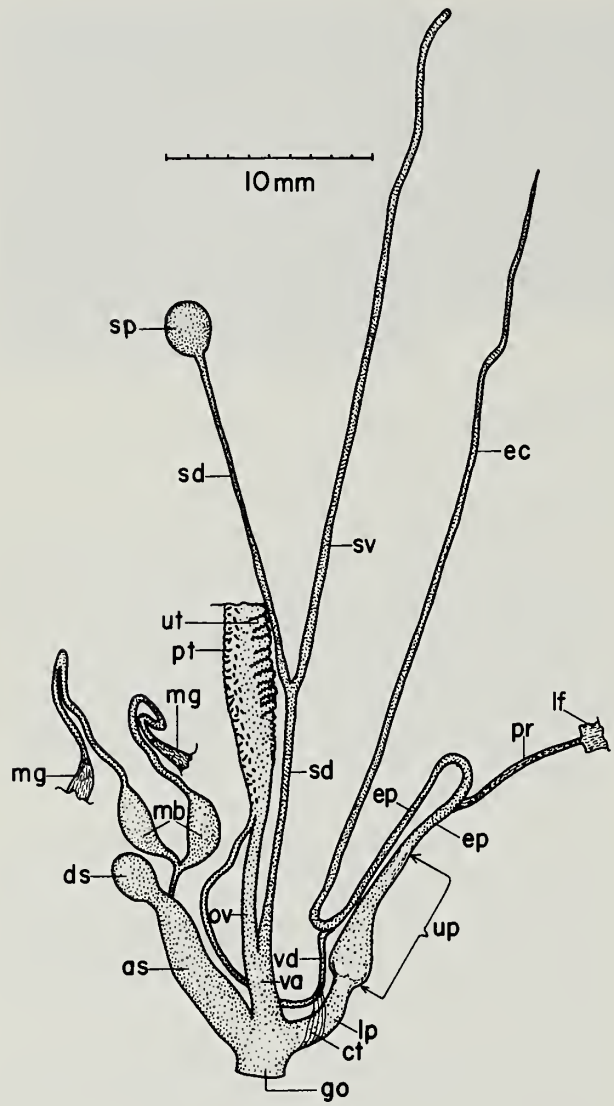

Figure 4

Helminthoglypta ***concolor***, anterior portion of reproductive system drawn from projection of stained whole mount; paratype SBMNH 34950. Arrows indicate limits of double-tubed upper chamber of penis. Abbreviations: as, atrial sac; ct, connective tissue binding penis to vas deferens; ds, dart sac; ec, epiphallic caecum; ep, epiphallus; go, genital orifice; lf, piece of floor of lung at origin of penial retractor muscle; lp, lower chamber of penis; mb, mucus gland bulbs; mg, initial portion of mucus gland membranes; ov, oviduct; pr, penial retractor muscle; pt, prostate (part); sd, spermathecal duct; sp, spermatheca; sv, spermathecal diverticulum; up, upper chamber of penis; ut, uterus (part); va, vagina; vd, vas deferens.

Remarks: In the material at hand, adult shell diameter ranges from 18.6 to 23.1 mm (mean of 15 specimens including holotype, 20.5 mm); height, 9.4 to 12.0 mm ($\bar{x}$ = 10.9 mm); height/diameter ratio, 0.50 to 0.58 ($\bar{x}$ = 0.53); width of umbilicus 2.0 to 3.1 mm ($\bar{x}$ = 2.7); number of whorls, 4.7 to 5.3 ($\bar{x}$ = 5.0). The number of embryonic whorls ranges from 1.75 to 1.9.

On well-preserved shells, the papillae on at least the first three whorls are surmounted by minute periostracal setae. The holotype shows no traces of spiral sculpture, but the base of one paratype has faint incised grooves which interrupt the growth rugae, and a second paratype has minor traces of incised spiral lines on the first neanic whorl.

Helminthoglypta ***concolor*** is similar to *Helminthoglypta* (*Coyote*) *isabella* Berry, 1938, from near Lake Isabella in the drainage of the Kern River, Kern County. Both species have broad, flat shells with body whorls increasing in diameter more rapidly than in any other species of *Coyote*. *Helminthoglypta isabella* differs in having a slightly more elevated spire. The last quarter-turn of the body whorl descends farther and there is a tendency toward a faint supraperipheral angulation. The inner lip of *H. isabella* encroaches slightly more on the umbilicus than that of *H.* ***concolor***. The base of *H. isabella* is usually as densely papillose as the shoulder of the whorl; in *H.* ***concolor***, the papillae usually become sparser on the base. The genitalia of both species are similar, but in *H. isabella* the common duct of the mucus glands is thicker-walled and the mucus bulbs less tumid; the anterior end of the upper chamber of the penis, while enlarged, is not as broadly swollen as in *H.* ***concolor***.

Helminthoglypta (*Helminthoglypta*) *piutensis* Willett, 1938, from the vicinity of Piute Mountain, Kern County, is also similar in shell shape but has the reproductive system anatomy of *Helminthoglypta, sensu stricto,* lacking the penis papilla and enlarged anterior end of the upper penial chamber. It was originally described as a subspecies of *Helminthoglypta* (*Rothelix*) *cuyamacensis* (Bartsch, 1916); Miller (1985) pointed out that it belongs to the typical subgenus and elevated it to the rank of species. The shell of *H. piutensis* has finer, more densely packed, more irregular papillation on the spire than *H.* ***concolor***. On parts of the body whorl the papillation gives way to short, low, irregular but mainly spirally directed ridges of periostracum. The surface between the papillae is densely wrinkled, producing a duller luster than that of *H.* ***concolor***.

Helminthoglypta isabella and *H.* ***concolor*** are the only species of the subgenus *Coyote* thus far described from the watershed of the San Joaquin Valley. All other species of the subgenus occur either on or around the fringes of the Mojave Desert or (*Helminthoglypta petricola* (Berry, 1916) and subspecies) in the mountains of San Bernardino, Los Angeles, Riverside, and Orange counties (Reeder & Roth, 1988). The distribution of the Mojave Desert species apparently reflects the ancient course of the Mojave River prior to the rise of the Transverse Ranges to their present elevation (Reeder & Roth, 1988). The ranges of *H.* ***concolor*** and *H. isabella* (or their common ancestor) also may have been within the Mojave River drainage before the uplift and westward tilting of the Sierra Nevada block displaced the San Joaquin/Mojave drainage divide eastward.

Before its main uplift, the Sierra Nevada was a broad ridge with summits of approximately 1000 m elevation (AXELROD, 1956, 1957). Although minor uplift took place as early as the Oligocene, the major elevation occurred in the late Tertiary (CHRISTENSEN, 1966; HAY, 1976; SLEMMONS *et al.*, 1979; HUBER, 1981) and the range did not exert a major effect on the distribution of vegetation until post-Pliocene time (AXELROD, 1962).

Fossil *Helminthoglypta* shells similar and possibly identical to the modern Mojave Desert species *Helminthoglypta* (*Coyote*) *graniticola* Berry, 1926, preserved in cherty limestones of the Cable Formation (of LAWSON, 1906) from 3.2 km north of Tehachapi (CAS 39352), 16 km north of the known range of *H.* ***concolor***, show that members of the subgenus *Coyote* were present in the area as early as the Pliocene. The Cable Formation consists of lacustrine rocks deposited before the formation of the present Tehachapi Valley, at a time when the main local drainage was from the north rather than northward as at present. Following orogeny of the Tehachapi Mountains, the headwaters of the former southward drainage were captured by erosion cutting back from the San Joaquin Valley into the upraised mountains (LAWSON, 1906).

Another fossil species, *Helminthoglypta* (*Coyote*) *alfi* Taylor, 1954, from the middle Miocene Barstow Formation, San Bernardino County, is located on the eastern edge of the modern range of the subgenus. It occurs in a molluscan assemblage indicating conditions more mesic than the highly arid Mojave Desert environment today.

It appears, therefore, that the distribution of the subgenus *Coyote*, including *Helminthoglypta* ***concolor***, antedates the present topography and the development of the diverse environments in which its component species now survive.

Etymology: L., ***concolor***, uniformly colored—alluding to the White Fir, *Abies concolor*, prominent at the type locality. All observations of *Helminthoglypta* ***concolor*** thus far have been in direct association with fir logs or bark on the ground.

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LITERATURE CITED

AXELROD, D. I. 1956. Mio-Pliocene floras from west-central Nevada. Univ. California Publ. Geol. Sci. 33:1-322, pls. 1-32.

AXELROD, D. I. 1957. Late Tertiary floras and the Sierra Nevadan uplift. Bull. Geol. Soc. Amer. 68(1):19-46.

AXELROD, D. I. 1962. Post-Pliocene uplift of the Sierra Nevada, California. Bull. Geol. Soc. Amer. 73(2):183-198.

CHRISTENSEN, M. N. 1966. Late Cenozoic crustal movements in the Sierra Nevada of California. Bull. Geol. Soc. Amer. 77(2):163-182.

HAY, E. A. 1976. Cenozoic uplifting of the Sierra Nevada in response to North American and Pacific plate interactions. Geology 4(12):763-766.

HUBER, N. K. 1981. Amount and timing of late Cenozoic uplift and tilt of the central Sierra Nevada, California—evidence from the upper San Joaquin River basin. U.S. Geol. Surv. Prof. Pap. 1197:iv + 28 pp.

KÜCHLER, A. W. 1977. The map of the natural vegetation of California. Pp. 909-939, map. *In:* M. G. Barbour & J. Major (eds.), Terrestrial vegetation of California. John Wiley and Sons: New York.

LAWSON, A. C. 1906. The geomorphogeny of the Tehachapi Valley system. Univ. California Publ. Bull. Dept. Geol. 4(19):431-462, pls. 42-51.

MILLER, W. B. 1985. A new subgenus of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae). Veliger 28(1):94-98.

REEDER, R. L. & B. ROTH. 1988. A new subgenus of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae) with the description of a new species from San Bernardino County, California. Veliger 31(3/4):252-257.

SLEMMONS, D. B., D. VAN WORMER, E. J. BELL & M. L. SILBERMAN. 1979. Recent crustal movements in the Sierra Nevada-Walker Lane region of California-Nevada: Part I, rate and style of deformation. Tectonophysics 52(1-4):561-570.

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A New Species of Tergipedid Nudibranch from Morro Bay, California

by

DAVID W. BEHRENS

Pacific Gas and Electric Company, Biological Research Laboratory,
P.O. Box 117, Avila Beach, California 93424, U.S.A.

AND

TERRENCE M. GOSLINER

Department of Invertebrate Zoology and Geology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118, U.S.A.

Abstract. Specimens of a new species of aeolidacean nudibranch, *Cuthona* ***rolleri,*** are described from the central coast of California. This species, although aberrant in its dorsoventrally flattened body, resembles other members of *Cuthona* in its internal characteristics. Although demonstrating some primitive features, *C.* ***rolleri*** is highly modified in most of its anatomy. Certain anatomical features suggest a burrowing lifestyle.

INTRODUCTION

The systematics of the Tergipedidae of the northeastern Pacific has been reviewed and revised by several authors in recent years (Williams & Gosliner, 1979; Gosliner, 1981; Gosliner & Millen, 1984; Behrens, 1984, 1985; Millen, 1986; Behrens, 1987). This paper describes the morphology of a new species of aeolidacean nudibranch belonging to the genus *Cuthona* Alder & Hancock, 1855. In addition to some primitive morphological characteristics, this species appears advanced in much of its morphology. It is unique owing to its apparent burrowing behavior under the surface of mud substrates.

Tergipedidae Thiele, 1931

Cuthona Alder & Hancock, 1855

Cuthona ***rolleri*** Behrens & Gosliner, sp. nov.

(Figures 1–4)

Morro Bay Aeolid: Behrens, 1980:105, fig. 162.

Type material: Holotype: California Academy of Sciences, CASIZ 064894, approximately 7 mm (preserved), collected intertidally, Morro Bay, California (35°22′N, 120°51′W), 18 August 1970, by Gary McDonald. **Paratypes:** (1) One specimen, dissected, CASIZ 064895, 7 mm (preserved), collected intertidally, Morro Bay State Park boat basin, Morro Bay, California (35°22′N, 120°51′W), 19 July 1970 by Gary McDonald. (2) One specimen, dissected, CASIZ 064896, 13 mm (preserved), collected intertidally, Morro Bay, California (35°22′N, 120°51′W), 26 April 1985 by L. L. Bud Laurent.

Distribution: Specimens are known from Piedras Blancas, northern San Luis Obispo County, to the southern portion of Morro Bay, San Luis Obispo County, California.

Etymology: The specific epithet, ***rolleri,*** is chosen to acknowledge the contributions made by Mr. Richard A. Roller in the field of opisthobranch biology, particularly those efforts centering on Morro Bay of the central coast of California, the type locality of this species.

Description

External morphology: The living animals (Figures 1, 2A) may reach 15 mm in length. The body is dorsoventrally flattened and elongate. The foot is very wide, approximately twice the width of the notum, and tapers posteriorly to a rounded tail. The rhinophores are simple, smooth, and tapering. The oral tentacles are moderately long, ta-

Figure 1

Cuthona ***rolleri*** Behrens & Gosliner, sp. nov., specimen collected November 1977 from Piedras Blancas, California, by David Laur. Photograph by Gary McDonald.

pering to a blunt end. Medially the oral tentacles are connected, forming an oral veil. The foot corners are rounded. The cerata are very long and flattened antero-posteriorly. Each ceras contains a small but distinct cnidosac at its apex. The cerata are arranged in five widely separated dorsolateral groups, set on slight elevations. The cerata are held nearly horizontal to the body and are closely apressed to the substrate. The cerata of the pre-pericardial group are arranged in six simple rows per side, while the posterior groups are in four simple rows per side (Figure 2). The ceratal formula of the specimen collected on 26 April 1985 is: I-2, II-2, III-4, IV-4, V-5, VI-5 (pre-pericardial) and VII-5, VIII-5, IX-4, X-3 (post-pericardial). The anus is acleioproctic, located on the right side of the body, immediately anterior to the most dorsal ceras of the first row of the right posterior digestive branch (Figure 2B). The nephroproct is located immediately dorsal to the anus on the anal papilla (Figure 2B). The gonopores are located on the right side of the body, ventral to the anterior first ceratal group.

The ground color of the body is white. The golden jaws and white central nervous system are readily visible in the head. The ceratal cores are salmon pink. The tips of the cerata are frosted white. There are very fine brown specks scattered over the surface of each ceras. In one specimen there was a single row of subcutaneous reddish spots between the ceratal insertions and the foot margin, from the anterior ceratal group to the tail.

Digestive system: The buccal mass is thick and muscular. The thick oval jaws (Figure 3A) are gold in color. Their masticatory border is long and arched, bearing a single row of 26–32 tall, bifurcate denticles (Figure 3B). In one specimen, the denticles appeared bristled. The radular formula is 23–31 × 0·1·0. The radular teeth (Figures 3C, D) are thin and elongate with a deep arch. On either side of the prominent, triangular central cusp are five to seven denticles.

Reproductive system: The reproductive system (Figure 4) is androdiaulic. The ovotestis consists of numerous hermaphroditic units, with a large central male acinus and about 10 smaller, peripheral female acini. From the ovo-

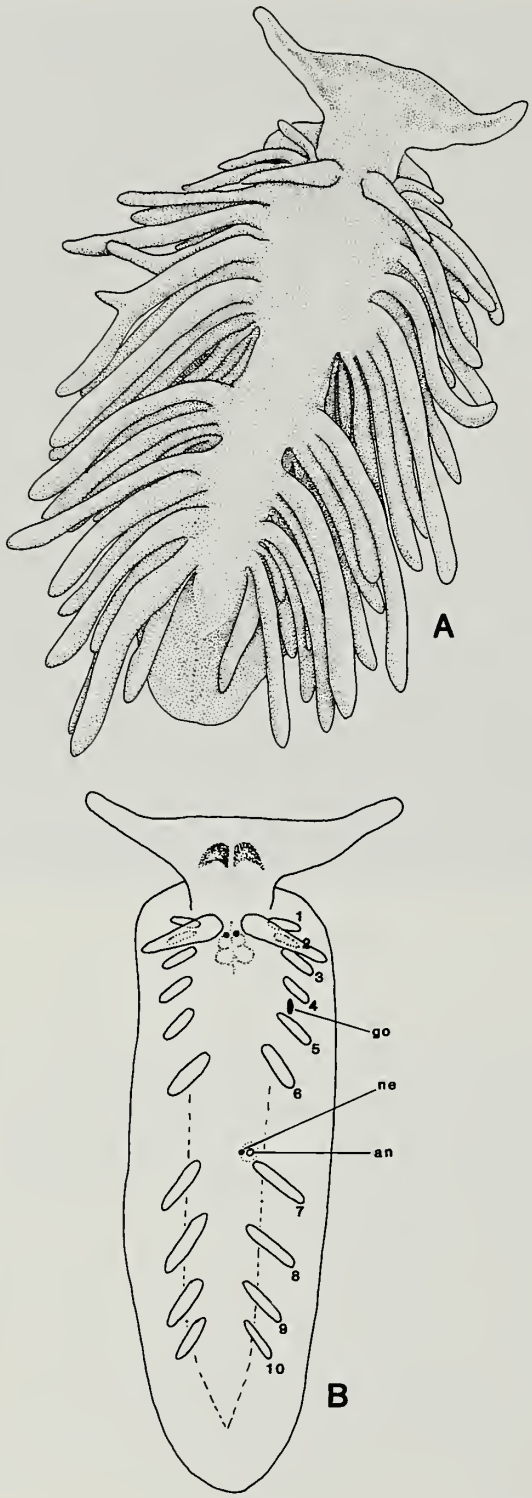

Figure 2

Cuthona ***rolleri***, sp. nov. A. Living animal drawn by Bruce Stuart, from color transparency. B. Dorsal view. Key: an, anus; go, genital orifice; ne, nephroproct; numbers designate ceratal groups.

testis, a narrow preampullary duct expands into a large saccate ampulla. The distal end of the ampulla bifurcates into the short oviduct and the longer vas deferens. The oviduct enters the female gland mass near the junction of albumen and membrane glands with the larger mucous gland. The vas deferens is narrow and does not appear prostatic. It enters the base of the penis. A spherical penial gland is present distal to the base of the penial papilla. The papilla is conical and unarmed, devoid of any chitinous stylet. A small, spherical receptaculum seminis joins the female gland mass, by means of a short stalk.

Natural history: Except for a specimen collected at Piedras Blancas, California, November 1977, by David Laur, all specimens were from shallow tidal pools on mud flats. The specimen collected on 16 August 1970 was found together with the burrowing cephalaspidean, *Acteocina inculta* (Gould, 1885) (Gary McDonald, personal communication). The broad head, wide foot, and flattened cerata appear to be adaptations for burrowing.

Discussion: Although the present species is aberrant in its external morphology, having a dorsoventrally flattened body and a broad oral veil, its internal characteristics closely resemble other members of the Tergipedidae. *Cuthona* ***rolleri*** has a uniseriate radula, acleioproctic anus, central male and peripheral female acini in the ovotestis, a penis with a rounded penial gland, and a receptaculum seminis situated proximally to the gonopore. All of these features clearly indicate that the present species is properly placed within the Tergipedidae.

Generic divisions within the Tergipedidae have been reviewed by Miller (1977), Williams & Gosliner (1979), Brown (1980), and Millen (1986). There is not universal agreement as to which genera are distinct, particularly relative to the genus *Catriona*. Miller (1977) and Brown (1980) considered *Catriona* Winkworth, 1941, as a junior synonym of *Cuthona* Alder & Hancock, 1855, while Williams & Gosliner (1979), Gosliner & Griffiths (1981), Edmunds & Just (1983), and Behrens (1984) maintain the distinctness of *Catriona*. Miller (1977) placed several tergipedid genera in synonymy with *Cuthona*, and Williams & Gosliner (1979) united *Precuthona* and *Cuthona* since it was determined that the type species of both genera are in fact synonymous. Most recently, Millen (1986) demonstrated that there is no distinct morphological gap between *Cuthonella* Bergh, 1884, and *Cuthona*. She also discussed primitive features within *Cuthona*. *Cuthona* ***rolleri*** is primitive in that it lacks a penial stylet and has a broad foot, but is modified in all other aspects of its morphology. It has simple rather than divided ceratal rows, a penial gland at the base of the penis rather than on the vas deferens, and a receptaculum seminis but no bursa copularix.

Cuthona ***rolleri***, based on several aspects of its morphology, is placed within the genus *Cuthona*. Members of several tergipedid genera, *Phestilla* Bergh, 1874, *Tergipes*

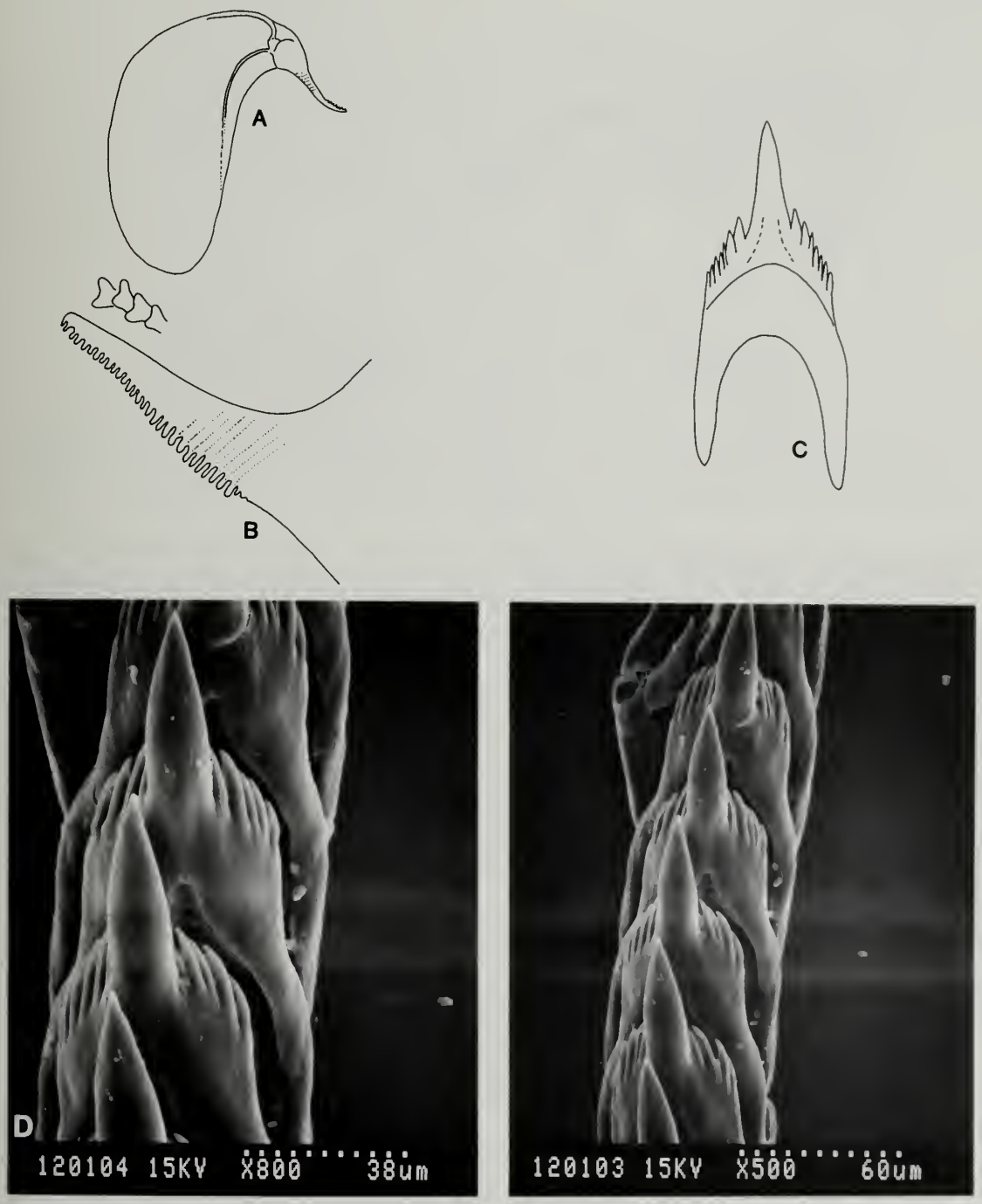

Figure 3

Cuthona ***rolleri,*** sp. nov. A. Jaw. B. Masticatory edge. C. Radular tooth. D. Scanning electron micrographs of radula.

Cuvier, 1805, *Tenellia* A. Costa, 1866, and *Catriona* Winkworth, 1941, bear some resemblance to *C.* ***rolleri***. Though similar in body form, species of *Phestilla* lack cnidosacs, have radular teeth with elongate denticles, and are specialized predators on scleractinean corals. Species of *Tergipes* have only a single ceras per ceratal branch. Members of the genus *Tenellia* entirely lack oral tentacles. Without exception, members of *Catriona* have pre-radular teeth which are absent in *C.* ***rolleri***. All species of these genera, except *Catriona rickettsi* Behrens, 1984, and the species

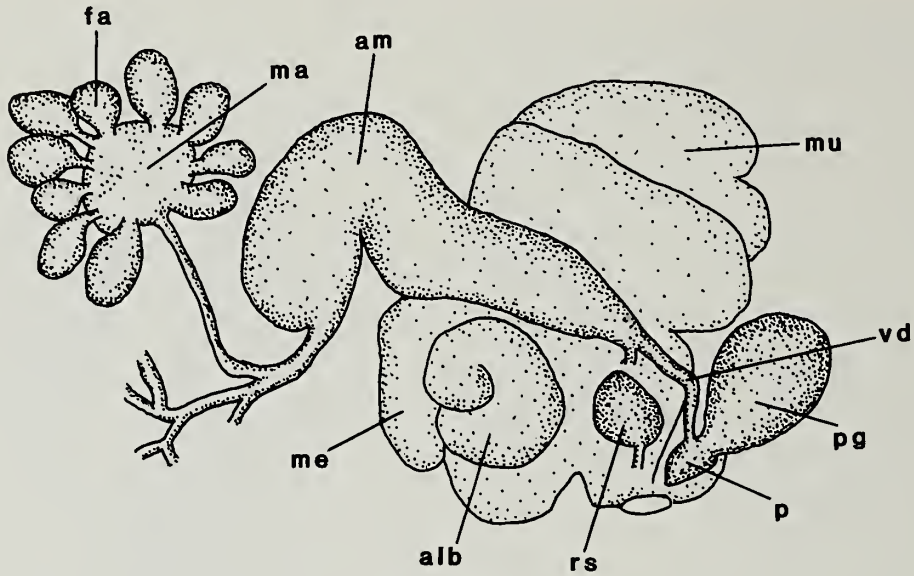

Figure 4

Cuthona ***rolleri,*** sp. nov. Reproductive system. Key: alb, albumen gland; am, ampulla; fa, female acini; ma, male acinus; me, membrane gland; mu, mucus gland; p, penis; pg, penial gland; rs, receptaculum seminis; vd, vas deferens.

described by MILLER (1977) as *Catriona alpha* (Baba & Hamatani, 1963) possess a penial stylet, while *C.* ***rolleri*** has an unarmed penis.

Cuthona ***rolleri*** can be clearly differentiated from all other described members of the genus, based on its unique dorsoventrally flattened body form, partially united cephalic tentacles, and cerata somewhat elevated on peduncles. Several other northeastern Pacific species of *Cuthona* have a broad foot and lack a penial stylet. However, they also possess other morphological characteristics not present in *C.* ***rolleri***. *Cuthona concinna* (Alder & Hancock, 1842) and *C. punicea* Millen, 1986, have a penial gland that inserts on the vas deferens rather than at the base of the penis. *Cuthona nana* (Alder & Hancock, 1842) and *C. divae* (Marcus, 1961) have compound, divided ceratal rows (WILLIAMS & GOSLINER, 1979; BROWN, 1980) when fully mature. *Cuthona cocochroma* Williams & Gosliner, 1979, is more narrow and elongate than *C.* ***rolleri***. It also has angular foot corners rather than the rounded anterior margin of the foot that is present in *C.* ***rolleri***.

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LITERATURE CITED

BEHRENS, D. W. 1980. Pacific coast nudibranchs. A guide to the opisthobranchs of the northeastern Pacific. Sea Challengers: Los Osos, California. 112 pp.

BEHRENS, D. W. 1984. Notes on the tergipedid nudibranchs of the northeastern Pacific, with the description of a new species. Veliger 27(1):65–71.

BEHRENS, D. W. 1985. A new species of *Cuthona* from the Gulf of California. Veliger 27(4):418–422.

BEHRENS, D. W. 1987. Two new aeolid nudibranchs from southern California. Veliger 30(1):82–89.

BROWN, G. H. 1980. The British species of the aeolidacean family Tergipedidae (Gastropoda: Opisthobranchia) with a discussion of the genera. Zool. Jour. Linn. Soc. 69(7):225–255.

EDMUNDS, M. & H. JUST. 1983. Eolid nudibranchiate Mollusca from Barbados. Jour. Moll. Stud. 49(3):185–203.

GOSLINER, T. M. 1981. A new species of tergipedid nudibranch from the coast of California. Jour. Moll. Stud. 47:200–205.

GOSLINER, T. M. & R. J. GRIFFITHS. 1981. Description and revision of some South African aeolidacean Nudibranchia (Mollusca, Gastropoda). Ann. S. Afr. Mus. 84(2):105–150.

GOSLINER, T. M. & S. V. MILLEN. 1984. Records of *Cuthona pustulata* (Alder & Hancock, 1854) from the Canadian Pacific. Veliger 26(3):183–187.

MILLEN, S. V. 1986. Northern, primitive tergipedid nudibranchs, with a description of a new species from the Canadian Pacific. Can. Jour. Zool. 64(6):1356–1362.

MILLER, M. C. 1977. Aeolid nudibranchs (Gastropoda: Opisthobranchia) of the family Tergipedidae from New Zealand waters. Zool. Jour. Linn. Soc. 60(3):197–222.

WILLIAMS, G. C. & T. M. GOSLINER. 1979. Two new species of nudibranchiate molluscs from the west coast of North America, with a revision of the family Cuthonidae. Zool. Jour. Linn. Soc. 67:203–223.

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New Hawaiian Species of Epitoniidae (Mollusca: Gastropoda)

by

HELEN DuSHANE

15012 El Soneto Drive, Whittier, California 90605, U.S.A.
Museum Associate, Natural History Museum of Los Angeles County

Abstract. Five new species of Epitoniidae from Hawaii are described: *Epitonium* ***hemmesi***, *E.* ***thorssoni***, *Asperiscala* ***goldsmithi***, *Opalia* ***burchorum***, and *Laeviscala* ***luceo***. *Epitonium* ***thorssoni*** and *Asperiscala* ***goldsmithi*** have been recognized in collections from other Indo-Pacific localities.

INTRODUCTION

Five species of Epitoniidae have been recognized as new to science in the course of preparation of a revision of the family in Hawaiian waters (DuShane, 1987a, b, 1988a, b, c). These new species are described in this paper.

Type specimens and other material of the new species have been located in the Thomas & Beatrice Burch Collection, Kialua, Oahu; DuShane Collection, Whittier, California; Don Hemmes Collection, Hilo, Hawaii; Merton Goldsmith Collection, Hilo, Hawaii; S. Jazwinski Collection, Honolulu; Wesley Thorsson Collection, Honolulu; and Arthur Weil Collection, Cincinnati.

Abbreviations for institutions mentioned in the text are as follows: AMNH, American Museum of Natural History, New York; BPBM, Bernice P. Bishop Museum, Honolulu; LACM, Los Angeles County Museum of Natural History; MHNG, Museum d'Histoire Naturelle, Geneva; USNM, United States National Museum, Washington, D.C.

Epitonium Röding, 1798

Type species (subsequent designation Suter, 1913): *Turbo scalaris* Linnaeus, 1758.

Shells are usually colorless, somewhat turreted, sometimes umbilicate, with axial sculpture of slender to heavy, sometimes recurved costae; whorls are numerous, with varying degrees of convexity, coiled either loosely or tightly. Spiral sculpture may be present or absent. The aperture is round to oval, with an operculum that is thin and paucispiral.

Epitonium (*s.l.*) ***hemmesi*** DuShane, sp. nov.

(Figures 1, 2)

Description: Shell small, maximum length 10.8 mm, globose, thin; protoconch glassy, dark, of 2–3 whorls; teleoconch of 7–8 rapidly expanding whorls, with reddish brown bands of unequal width; suture distinct; costae 11–12 on last whorl, white; 8 unevenly spaced crenulations on each costa; approximately 10 heavy, white spiral cords between costae, sometimes with unevenly spaced, fine, spiral striae between cords; aperture circular, lip slightly reflected, with uneven crenulations on outer edge; umbilicus lacking, operculum unknown.

Dimension of holotype: Length 8.6 mm, width 4.2 mm.

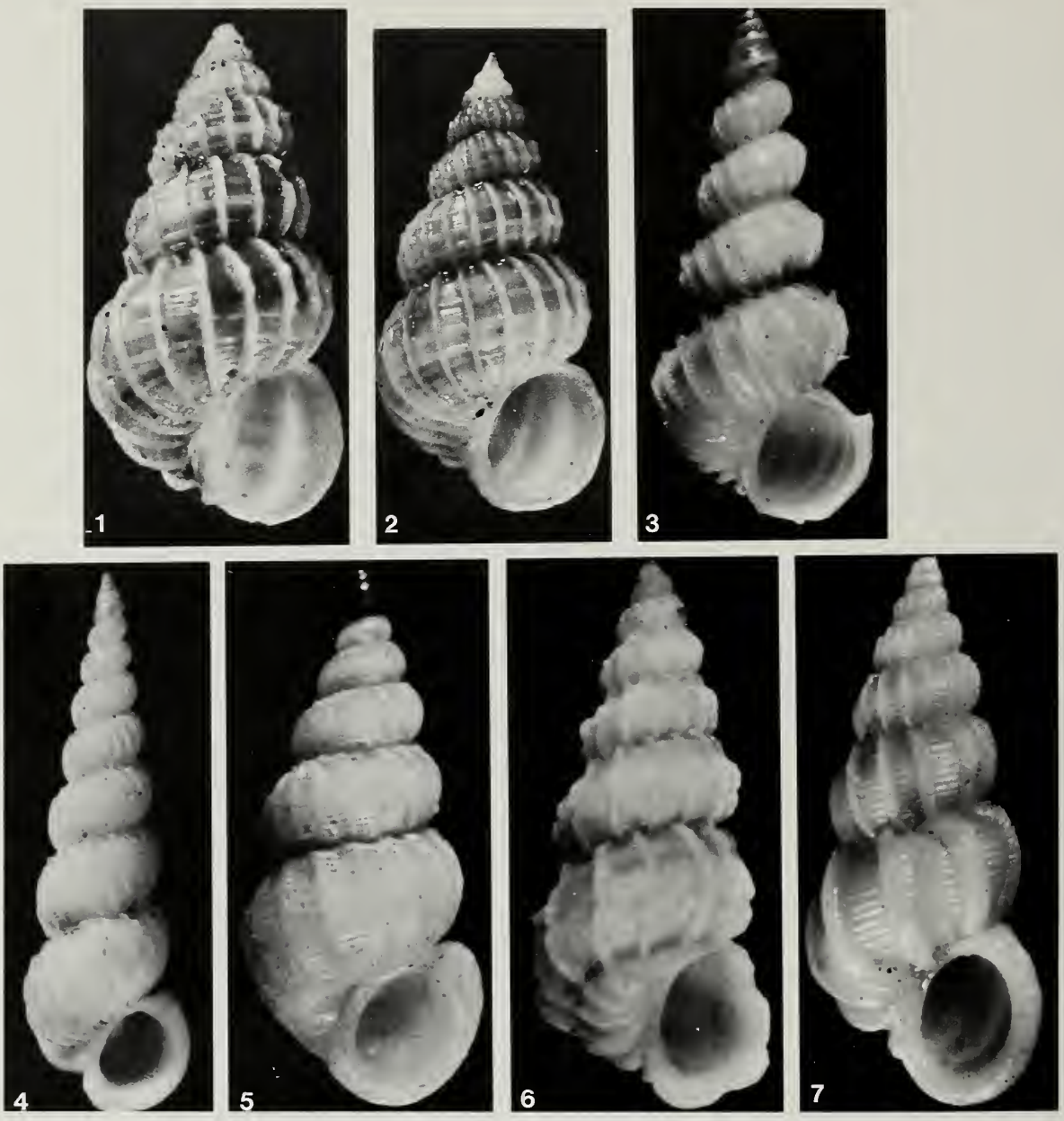
Type locality: Lahilahi Point, near Makaha Beach, Oahu, Hawaii (21°28.0′N, 158°14.2′W), 20–27 m, rubble.

Type material: Thirteen specimens collected at type locality by D. Hemmes and S. Jazwinski, 1985–1986. Holotype, BPBM 8987; 1 paratype, BPBM 8988 (length 3.8 mm); 2 paratypes, AMNH 225995 (lengths 7.0, 4.0 mm); 2 paratypes, LACM 2306 (lengths 10.8, 3.9 mm); 3 paratypes, DuShane Collection (lengths 9.3, 4.7, 3.3 mm); 2 paratypes, Hemmes Collection (lengths 9.5, 2.1 mm); 1 paratype, Goldsmith Collection (length 4.2 mm); 1 paratype, Jazwinski Collection (length 7.7 mm).

Referred material: One specimen, Hemmes Collection, Puhi Bay, Hawaii Island, 5 m.

Discussion: No other epitoniid has the distinctive characters of this species: the reddish-brown bands (faded on dead-collected specimens), heavy spiral cords with unevenly spaced fine spiral striae between the costae, and the crenulated, slightly reflected costae. *Epitonium* ***hemmesi*** does not fit comfortably into any of the generic or subgeneric taxa in the family. I therefore assign it to the genus in the broad sense.

The name honors Don Hemmes, Division of Natural Sciences, University of Hawaii at Hilo, Hawaii.



Explanation of Figures 1 to 7

Figure 1. *Epitonium* ***hemmesi,*** sp. nov. Paratype, DuShane Collection. Lahilahi Point, Makaha Beach, Oahu, Hawaii. Length 9.3 mm.

Figure 2. *Epitonium* ***hemmesi,*** sp. nov. Holotype, BPBM 8987. Lahilahi Point, Makaha Beach, Oahu, Hawaii. Length 8.6 mm.

Figure 3. *Asperiscala* ***goldsmithi,*** sp. nov. Loosely coiled variant, Burch Collection. Mamala Bay, Oahu, Hawaii. Length 3.0 mm.

Figure 4. *Aperiscala* ***goldsmithi,*** sp. nov. Holotype, LACM 2304. Puhi Bay, Hilo, Hawaii. Length 6.4 mm.

Figure 5. *Opalia* ***burchorum,*** sp. nov. Holotype, BPBM 8974. Off Kahe Point, Oahu, Hawaii. Length 4.0 mm.

Figure 6. *Epitonium* ***thorssoni,*** sp. nov. Holotype, BPBM 8986. Makaha Beach, Oahu, Hawaii. Length 2.8 mm.

Figure 7. *Laeviscala* ***luceo,*** sp. nov. Holotype, BPBM 8989. Sand Island, Oahu, Hawaii. Length 3.4 mm.

Epitonium (*s.l.*) ***thorssoni*** DuShane, sp. nov.

(Figure 6)

Description: Shell minute, maximum length 3.5 mm; protoconch whorls 3, glassy; teleoconch whorls 5, white, shining, distinctly angled, with 2 diffused brown bands on each whorl between costae, one on base and one on upper half of last whorl, brown bands becoming fainter on early whorls; costae 13, heavy, continuing into aperture, each with 5–7 scallops; 5 heavy spiral cords between costae on last whorl, each recurved at base of last whorl, almost forming a basal ridge; suture deep; aperture large; reflected lip heavy, with 7 scallops; operculum unknown.

Dimensions of holotype: Length 2.8 mm, width 1.6 mm.

Type locality: Off S side Oahu Island, Hawaii (21°15.8′N, 157°50′W), 62–80 m, silty sand.

Type material: Four specimens from type locality, dredged by Wesley Thorsson, 1980, 1981, 1985. Holotype, BPBM 8986; 2 paratypes, LACM 2302 (lengths 2.6, 1.6 mm); 1 paratype, DuShane Collection (length 3.5 mm).

Referred material: Hemmes Collection, Puhi Bay, Hawaii Island, 6 m; LACM 74-67, NW end Lanai Island, Hawaii, 18 m; LACM 77-13, Apra Harbor, Guam, Mariana Islands, 2 m; LACM 84-161, Ani Lao, Batangas Province, Luzon, Philippines, 25 m; LACM 85-112, Sinai Peninsula, Egypt, northern Red Sea, 25 m.

Discussion: There are no epitoniids that are directly comparable to this species. As with the preceding species, it is assigned to *Epitonium* in the broad sense. The distinctive characters are the brown banding, which becomes stronger on later whorls, and the scalloped costae. It is vaguely reminiscent of *Cirsotrema zelebori* (Dunker, 1886), from New Zealand (Powell, 1979:252, pl. 48, fig. 17), but it has a much smaller shell and does not have the well-defined basal ridge of that species. *Epitonium* ***thorssoni*** has remained undescribed until now probably because of its small size.

The name honors Wesley M. Thorsson of Honolulu, who has collected extensively in the Hawaiian Islands.

Asperiscala deBoury, 1909

Type species (original designation): *Scalaria bellastriata* Carpenter, 1864.

Shell white or pink to dark gray or brown; costae usually recurved, sometimes with a spine on whorl shoulder; sculpture of heavy spiral cords to fine striations, sometimes obsolete on later whorls.

Asperiscala has been used as a subgenus of *Epitonium* and as a full genus by DuShane (1979).

Asperiscala ***goldsmithi*** DuShane, sp. nov.

(Figures 3, 4)

Description: Shell small, maximum length 7.5 mm, white, thin, elongate; protoconch whorls 5, glassy, dark, the 5th whorl extremely bulbous and skewed to make entire protoconch tilted with respect to the shell axis; teleoconch whorls 6–8, angulate below suture; costae 18–24, oblique, thin, reflected, angulate near suture and with scattered heavier costae; small sharp spines on shoulder whorl; interspaces spirally striate, striae easily seen without magnification, 20–22 between costae on last whorl; suture deep; aperture oval; lip slightly reflected, with small spine on inner base of aperture.

Dimensions of holotype: Length 6.4 mm, width 1.8 mm.

Type locality: Puhi Bay, Hilo, Hawaii (19°44′N, 155°03′W), intertidal.

Type material: Ten specimens from type locality collected by M. Goldsmith, 1983. Holotype, LACM 2304; 2 paratypes, LACM 2305 (lengths 7.4, 5.2 mm); 2 paratypes, AMNH 225994 (lengths 6.1, 4.4 mm); 5 paratypes, DuShane Collection (lengths 7.5, 4.7, 3.8, 4.1, 4.0 mm, all but the largest broken at either or both ends).

Referred material: Hawaiian Islands: Burch Collection, 11 specimens from Burch stations 76064, 77017, 78001, 78020, 79024, 79072, 79073, 80093, Mamala Bay, Oahu, 18–468 m, and Burch station 80069, Kailua Bay, Oahu, 69–37 m; Goldsmith Collection, 1 specimen, Puako, W side Hawaii Island, intertidal; Hemmes Collection, 4 specimens, Kapoho, E side, Hawaii Island, intertidal; Hemmes Collection, 9 specimens, Sand Island, Oahu, 75 m; LACM 74-63, 1 specimen, off Koko Head, Oahu, 56 m; LACM 59-16, 1 specimen, off Molokini Island, S side Maui, 54 m; LACM 75-112, 2 specimens, Maalaea Bay, Maui, 18 m.

Other localities: LACM 80-12, 1 specimen, Astrolabe Bay, Papua New Guinea, 4 m; LACM 79-40, 1 specimen, Suva, Viti Levu, Fiji, 1 m; LACM 85-8, 1 specimen, Mai Thon Island, Phuket Island, Thailand, 3–15 m; LACM 85-14, 1 specimen Pee-Pee Island, off Phuket Island, Thailand, 15 m; LACM 83-7, 1 specimen, South Male Atoll, Maldive Islands, 16 m.

Discussion: The distinctive characters of *Asperiscala* ***goldsmithi*** are its small size (length 6 mm, width 2 mm), skewed protoconch, large number of costae with scattered heavier costae, sharp shoulder spine, and the oblique orientation of costae. Sometimes the whorls are partially disjunct, but this is not considered to be taxonomically significant, as there are a number of epitoniid species with this trait.

This small species is somewhat similar in outline to *Epitonium eusculptum* (Sowerby, 1903) from Japan (see Kuroda *et al.*, 1971:256, pl. 63, fig. 13), although that species has a much larger shell (20 mm in length) and is umbilicate. It is surprising that a species as common as this should have been overlooked, but again this is most likely because of its small size.

The name honors Merton Goldsmith of Hilo, Hawaii.

Opalia Adams & Adams, 1853

Type species (subsequent designation of deBoury, 1886): *Scalaria australis* Lamarck, 1822.

Shell white or light gray to brown, solid, imperforate; axial sculpture of strong ribs that may sometimes be angulated, with or without basal ridge and with spiral sculpture of fine threads and rows of small pits; chalky outer layer (intritacalx) over entire shell easily abraded; oval aperture oblique; lip thickened by final axial rib; operculum paucispiral.

Opalia (*s.l.*) ***burchorum*** DuShane, sp. nov.

(Figure 5)

Description: Shell small, maximum length 4.1 mm, bulbous, solid; protoconch dark, glassy, whorls 4; teleoconch whorls 6; strongly convex at periphery; costae 11, extending from whorl to whorl, continuous but indistinct on base; ribs and intervals sculptured with small punctations, 19 rows on last whorl, between minute, rounded, spiral cords; suture distinct, crenulated by crests of costae; base defined by rounded cord; aperture oval, oblique; peristome thick, with 15 rows of small punctations; operculum unknown.

Dimensions of holotype: Length 4.1 mm, width 2.0 mm.

Type locality: Off Kahe Point, Oahu, Hawaii (21°21.2′N, 158°09.1′W), 540 m, fine sand.

Type material: Five specimens from the type locality, Burch station 78019, dredged by T. & B. Burch, March 1978. Holotype, BPBM 8974; 1 paratype, USNM 859310 (length 3.1 mm); 1 paratype, LACM 2303 (length 4.1 mm); 1 paratype, Burch Collection (length 3.8 mm); 1 paratype, DuShane Collection (length 3.7 mm).

Discussion: *Opalia* ***burchorum*** differs from *Nodiscala mormulaeformis* Masahito, Kuroda & Habe, 1971, from Sagami Bay, Japan (KURODA *et al.*, 1971:248, pl. 63, fig. 1) in its more bulbous outline and smaller size. *Opalia* (*Opalia*) *abbotti* CLENCH & TURNER, 1952 (p. 348) resembles *O.* ***burchorum***, but the former, from Puerto Tanamo, Cuba, 540 m, has a more elongate shell, with more numerous whorls. *Scala* (*Cirsotrema*) *mammosa* Melvill & Standen, 1903, from the Gulf of Oman, is similar, but has a mammilate protoconch, fewer costae, and no basal disk.

The limits of the subgenera of *Opalia* are not clear and I choose to place this species in *Opalia* in the broad sense. *Opalia* ***burchorum*** occurs at greater depths than other species of *Opalia* in the Indo-Pacific.

The name honors Thomas and Beatrice Burch, of Kialua, Oahu, Hawaii.

Laeviscala deBoury, 1909

Type species: *Scalaria subauriculata* Souverbie, in Souverbie & Montrouzier, 1886.

Suture imperforate, umbilicus closed; axial ribs few, thick, reflexed, intervals with dense spirals.

Laeviscala has been treated as a full genus by COTTON (1959) and KURODA *et al.*, (1971).

Laeviscala ***luceo*** DuShane, sp. nov.

(Figure 7)

Description: Shell small, maximum length 3.7 mm, solid, broadly pyramidal, glistening; protoconch bulbous, whorls 2–3; teleoconch whorls 6–7; suture not deep; costae 9–10, thick, moderately recurved, unevenly spaced, dipping into suture; interspaces spirally striate, easily seen without magnification, 16–18 on last whorl; peritreme heavy, thick; aperture oval; operculum unknown.

Dimension of holotype: Length 3.4 mm, width 1.5 mm.

Type locality: Off Sand Island, S side Oahu, Hawaii (21°16.3′N, 157°50.7′W), 17 m, sand.

Type material: Five specimens from type locality dredged by S. Jazwinski, from Hemmes Collection. Holotype, BPBM 8989; 1 paratype, LACM 2325 (length 3.3 mm); 1 paratype, Hemmes Collection (length 3.2 mm); 2 paratypes, DuShane Collection (lengths 3.7, 3.7 mm).

Referred material: Three specimens, Burch Collection, Mamala Bay, Oahu, stations 75025, 79072, 43 m, sand and *Pinna* beds; 1 specimen Burch Collection, Kealaikahiki Channel, Hawaii Island, station 79065, 61 m, sand and *Pinna* beds.

Discussion: Compared to *Laeviscala subauriculatum*, the type species of the genus, *L.* ***luceo*** has a more sturdy, broader shell, with a well-defined suture, thicker, more numerous costae, and coarser spiral striations that are not microscopically decussated as in the type species. This epitoniid differs from all others in the Hawaiian fauna by its glistening appearance. The name ***luceo*** is Latin, meaning "glistening."

ACKNOWLEDGMENTS

I am grateful to Thomas Burch and Beatrice Burch for the privilege of studying their material, to Don Hemmes, Merton Goldsmith, Wesley Thorsson, Arthur Weil, and the Natural History Museum of Los Angeles County for allowing me to study and draw conclusions from their many specimens, and to R. N. Kilburn of the Natal Museum for helping to assess several of the puzzling species. My thanks to Bertram Draper for the excellent photographs and to James H. McLean for suggestions and for word-processing the manuscript.

LITERATURE CITED

CLENCH, W. J. & R. D. TURNER. 1952. The genera *Epitonium* (Part II), *Depressiscala, Cylindriscala, Nystiella,* and *Solutiscala* in the western Atlantic. Johnsonia 2(31):289–386.

COTTON, B. C. 1959. South Australian Mollusca, Archaeogastropoda. Government Printer: Adelaide. 449 pp.

DuShane, H. 1979. The family Epitoniidae (Mollusca: Gastropoda) in the northeastern Pacific. Veliger 22(2):91–134.

DuShane, H. 1987a. Classification of three species of Epitoniidae found in Hawaiian waters. Hawaiian Shell News 35(6):1, 4.

DuShane, H. 1987b. The many synonymic names of *Gyroscala lamellosa* (Lamarck, 1822). Hawaiian Shell News 35(11): 12.

DuShane, H. 1988a. Hawaiian Epitoniidae [Part 1]. Hawaiian Shell News 36(2):3–4.

DuShane, H. 1988b. Hawaiian Epitoniidae [Part 2]. Hawaiian Shell News 36(4):1, 7.

DuShane, H. 1988c. Hawaiian Epitoniidae [Part 3]. Hawaiian Shell News 36(5):9–10.

Kuroda, T., T. Habe & K. Oyama. 1971. The seashells of Sagami Bay. Maruzen: Tokyo. xvi + 741 + 489 pp., 121 pls.

Melvill, J. C. & R. Standen. 1903. The genus *Scala* (Klein) as represented in the Persian Gulf, Gulf of Oman, and North Arabian Sea, with descriptions of new species. Jour. Conch. 10(12):345–351, pl. 7.

Powell, A. W. B. 1979. New Zealand Mollusca; marine, land, and freshwater shells. Collins: Auckland. xiv + 500 pp.

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NOTES, INFORMATION & NEWS

Northern Range Extension for *Vitrinella floridana* Pilsbry & McGinty (Gastropoda: Prosobranchia: Vitrinellidae) from South Florida to the James River, Virginia[1]

by
Kevin J. McCarthy and Carrollyn Cox
Virginia Institute of Marine Science,
School of Marine Science,
College of William and Mary,
Gloucester Point, Virginia 23062, U.S.A.

Vitrinella floridana Pilsbry & McGinty, 1946, is a planorbid marine gastropod which may reach a diameter of 2.1 mm (Ode, 1987). This minute gastropod is found living under rocks from the intertidal zone (Abbott, 1974) to a depth of 45 m (Ode, 1987). Moore (1964) reported *V. floridana* to range from southern Florida and Texas to Campeche Bank, Mexico. Vokes & Vokes (1983) collected the snail from northeastern Yucatan and Belize. A more northern population of *V. floridana* in the James River, Virginia, is reported in this paper.

Monthly benthic samples were collected from 4 X 84 through 13 VIII 85 on a subtidal oyster reef, Wreck Shoal, in the James River (37°03.2'N, 76°34.6'W). Mean water depth at Wreck Shoal is approximately 3 m at mean low water. During the study, the bottom water temperature ranged from 27.1 to 3.7°C, and the salinity ranged from 20.4 to 12.4‰. The substrate at Wreck Shoal is a composite of oyster shell, shell fragments, and sandy mud. Collections were made with a suction sampler (Larsen, 1974) which removes bottom material from an area of 126 cm^2. One hundred twenty-six (126) of the living gastropods collected were *Vitrinella floridana*; shell diameters ranged from 0.7 to 1.5 mm. Specimens have been deposited at the Philadelphia Academy of Natural Sciences (ANSP# A12188C).

Identification of a population of *Vitrinella floridana* living in the James River is significant in several respects. *Vitrinella floridana* was considered to live in warm, high salinity waters (Moore, 1964) as far north as the Indian River, south of Sebastian, Florida (Pilsbry & McGinty, 1946). The James River population represents a range extension of approximately 1100 km north of this location. Moore (1964) postulated that vitrinellids could invade northern waters during warm months, but would die of natural causes before the water temperature dropped significantly. In this study, live individuals of *V. floridana* were found throughout the winter, with the highest abundance (30/sample) collected on 11 II 85 when the water temperature was 3.7°C. Salinities in the James River are significantly lower than those reported at other collection sites (*e.g.*, Moore, 1964).

Studies of oyster reef fauna usually target known oyster predators such as oyster drills, and the ectoparasite *Boonea impressa* (Say, 1822). *Vitrinella floridana* is very small and easily overlooked; this may explain the lack of reports of this species along the mid-Atlantic coast.

Acknowledgments

The authors would like to thank Dr. Donald R. Moore for his interest, assistance, and encouragement, and for identifying our samples of *Vitrinella floridana*. We are indebted to Ray Morales-Alamo and Kenneth Walker for their assistance in the field and to Ya-Ke Hsu for help with processing the samples. We would also like to thank Dr. Roger Mann for his review of the manuscript. This work was funded by a grant to VIMS from the Commonwealth of Virginia.

Literature Cited

Abbott, R. T. 1974. American seashells. 2nd ed. Van Nostrand Reinhold Co.: New York. 663 pp.

Larsen, P. F. 1974. A remotely operated shallow water benthic suction sampler. Chesapeake Sci. 15:176–178.

Moore, D. R. 1964. The family Vitrinellidae in south Florida and the Gulf of Mexico. Ph.D. Dissertation, The University of Miami, Coral Gables, Florida. 230 pp.

Ode, H. 1987. Distribution of records of the marine Mollusca in the northwest Gulf of Mexico. Texas Conch. 23(4):110–121.

Pilsbry, H. A. & T. L. McGinty. 1946. Vitrinellidae of Florida, part 4. Nautilus 60(1):12–18.

Vokes, H. E. & E. H. Vokes. 1983. Distribution of shallow water marine Mollusca, Yucatan Peninsula, Mexico. Mesosamerican Ecology Institute, Monograph 1, Middle American Research Institute. Publication 54. 1983:i–viii + 183 pp.

[1] Contribution Number 1446 from the Virginia Institute of Marine Science, College of William and Mary.

Soviet Contributions to Malacology in 1982

by
Kenneth J. Boss
Museum of Comparative Zoology,
Harvard University,
Cambridge, Massachusetts 02138, U.S.A.
and
M. G. Harasewych
Department of Invertebrate Zoology,
National Museum of Natural History,
Smithsonian Institution,
Washington, D.C. 20560, U.S.A.

As in previous synopses of the Soviet malacological literature (see Veliger 29[3]:340–348 for the most recent pre-

vious listing and reference to earlier ones), we offer a translation of the original titles and a summary of the work as abstracted in the Referativnyy Zhurnal in 1982. Generally speaking, we have utilized the categorizations employed by the Referativnyy Zhurnal.

Several papers established new genus- and species-level taxa, not only in the fauna of the Soviet Union but in other faunas. These include: Tavasieva on helicoid land snails of the Caucasus; Johansen and Starobogatov on triculids from Siberia; Izzatullaev on bithyniids from Central Asia; Stadnichenko on finger-nail clams (Cycladidae or Sphaeridae) from the Ukraine; and Chistikov on entalinid scaphopods.

Drastic shifts in the system of classification of prosobranch gastropods were introduced by Sitnikova and Starobogatov, who significantly altered previously accepted systems by allying the cowries and viviparids into a group called the Vivipariformii. This group is placed in an even higher taxon, the Archeotaenioglossa, erected on the basis of radular characters. Several family-level taxa are transferred from one order to another, and the authors have elevated the traditionally recognized subfamilies of viviparids into families.

General faunistic studies include delineations of the molluscan faunas of particular zoogeographic areas in the Soviet Union: Grundrizer recorded 55 species in Kureyka Lake of the Yenisey Basin in Siberia; Karabeili, 64 species in the Caspian Sea; Shikov, 51 species of land mollusks in the Valdai Hills; Zatravkin, 93 species in Seliger Lake of the Upper Volga; and Zatravkin and Bogatov, 69 species in the Amur River drainage of Siberia.

Interesting biological and ecological analyses include those of Sergievskii on *Littorina obtusata* in the White Sea and the Stadnichenkos on lymnaeids in the Crimea. Augmenting the classical work of Bondeson on the egg capsule morphology of freshwater pulmonates, Berezkina and Starobogatov have developed a new descriptive terminology for the encapsulated eggs of lymnaeid gastropods.

Among studies dealing with the Bivalvia, the analysis of the morphology of *Clencharia* by the late Dr. Z. Filatova and her colleague Dr. A. A. Shileiko constitutes an important contribution to the knowledge of protobranch anatomy. Kulikova *et al.* provide a description of the larval morphology of three different species of pectinids from the Far East.

In studies relating to cephalopods, Nesis has made two important contributions. One, an overview of the currently accepted higher taxonomic units within the Class, concludes that this systematic scheme reflects the true phyletic relationships of these animals. The other analysis constitutes a delineation of zoogeographic regions and zones of the world's oceans based on the distribution of cephalopods.

ABBREVIATIONS

BMV—Biologiya Morya (Marine Biology, Vladivostok)
ES—English Summary
GZ—Gidrobiologicheskii Zhurnal (Hydrobiological Journal)
SID—Sbornick Rabot Institute biologiya morya Dal'nevost. nauch. tsentr. Akad. Nauk. SSSR (Papers of the Marine Biological Institute of the Far Eastern Scientific Center, Academy of Sciences, USSR)
ZEBF—Zhurnal Evolyutsionnoi biokhimii i fiziologii (Journal of evolutionary biochemistry and physiology)
ZOB—Zhurnal Obshchey Biologii (Journal of General Biology)
ZZ—Zoologicheskii Zhurnal (Zoological Journal)

GENERAL

GUNDRIZER, V. A. 1981. Studies of the malacofauna of Kureyka Lake (Lower Yenisey Basin). Ekol.-faunistich. issled. Sibiri [Ecological and Faunistic Studies in Siberia] Tomsk, pp. 90–94.

[New data are presented on the freshwater malacofauna of the Kureyka River. Fifty-five species of mollusks are reported from the waterways of the region (16 for the first time from the Lower Yenisey Basin); examined are their roles in the diets of fish, and their ecological and zoogeographic affinities. Systematically, the mollusks belong to 7 families: Valvatidae (2 species); Bithyniidae (2); Lymnaeidae (18); Physidae (18); Bulinidae (2); Planorbidae (8); Pisidiidae (18). Zoogeographically, the mollusks have representatives of 4 faunal regions: Holarctic (4 species); Euro-Siberian (39); Asiatic (1); Siberian (11).]

IZZATULLAEV, Z. 1981. On the study of ecological groupings of freshwater mollusks from the eastern Pamirs. Krugovort Veshchestva i energii v vodoemakh. Tez. Doklady k 5-y Vses Limnol. Listvenichnoe na Baikala [Thesis Reports of the Fifth Annual All-Union Society of Limnology. Leaflets on Baikal], Vol. 2, Irkutsk, pp. 135–136.

[Thirty-one species of freshwater mollusks, both gastropods and bivalves, inhabiting lakes, rivers and thermal springs, are found in the eastern Pamirs. The species are categorized according to ecological preferences.]

KARABEILI, O. Z. 1981. Gastropod mollusks of the Central and Southern Caspian Sea. Vozdeistvie antropogen faktorov na faunu i ekol. zhivotnikh v Aserbaidzhane [Influence of human factors on the fauna and ecology of Azerbaijan] Baku, pp. 87–96.

[Sixty-four species of gastropods were collected in 321 benthic samples from the Central and Southern Caspian Sea. There were 53 species in the Central Caspian, of which 24 were characteristic, while 10 were characteristic in the Southern Caspian, which has 40 species. Data include: depth, optimal substrate, and percent occurrence. It is suggested that *Caspia gmelini* and *C. isseli* are subspecies of the same species, as are *C. schorygini* and *C. nana*. Twelve groups of gastropods are distinguished based on the breadth of their distributions (from those broadly distributed along the Central and Southern Caspian to those occurring only in the eastern or western portion of one region). Also included are data on the distribution of species by depth, the number of species per sample and the percent of species occurring on the various substrates.]

KHOKHUTKIN, I. M. & YU. A. EL'KIN. 1982. Experimental application of binary relationships for the estimation of resemblance of biotic associations using terrestrial mollusks as models. Phenetika Populyatsii (Population Phenetics), Moscow, pp. 125–132.

[Nine hundred seventy-five species of terrestrial mollusks were used in a study correlating characters of the shell with systematic-phylogenetic systems.]

LYURIN, I. B. & V. M. ZAKALYUZHNYI. 1982. Observations on the distribution of the malacofauna in the central basin of the Dnieper River. Materials for the Second Scientific Conference of Molluscan Research. Geological Series. Odessa, pp. 91–94.

[The ecological features of the distribution of the molluscan fauna of this area are given; special emphasis is paid to the reservoirs and other important habitats of aquatic invertebrates along the central Dnieper. The potential utility of these mollusks as food is discussed.]

NIKOLAEV, V. A. 1981. History of the study of the terrestrial molluscan fauna of the Central Russian Hills. Nauch. Tr. Kursk Ped. In-ta [Scientific Transactions of the Kursk Pedagogical Institute] 210:65–70.

[An historical review of studies on the molluscan fauna of this region, beginning with the work of Dvigubsky (1831) and including subsequent studies, such as regional reviews and taxonomic monographs, is presented.]

SHIKOV, E. V. 1981. Mollusks of the coniferous forests of the Valdai Hills and adjacent territories. "Fauna of the Upper Volga, its conservation and utilization" Kalinin, pp. 28–45.

[The malacofauna of coniferous forests in 29 regions of Kalinin and Novgorod Provinces was found to consist of 51 terrestrial species. The most speciose fauna is encountered in forests of average moisture, with thick grass cover and well developed deciduous subforest and shrubbery. Ecologically, particular land snails have preferences for certain types of plant associations or well defined phytocenoses.]

YAROSLAVTSEVA, L. M. 1981. A method for determining the limits of the osmoregulatory mechanism in marine mollusks. Inst. Marine Biol. Far Eastern Science Center, Acad. Sci. USSR. Manuscript [no pagination given].

[Preparations of ciliated epithelium from ctenidia were exposed to solutions of different salinities; changes in the beating of the cilia were correlated with changes in salinity, and a graphic analysis of the loss of activity is presented. This simplified method does not require elaborate or specialized equipment, and can be used under field conditions.]

ZATRAVKIN, M. N. 1981. Mollusks of the Upper Volga and Seliger Lake. ZZ 60(12):1878–1881 (ES).

[During a 1973 survey of the nearshore zone of the Upper Volga Lakes (Upper Volga Reservoir) and Lake Seliger, 79 species of mollusks were collected from 10 lakes and the lower portions of rivers and streams that fall into them. The reservoir was formed in 1843 as a result of the construction of a dam above where the Selizharovka River leaves Lake Seliger. As the Upper Volga Lakes are interconnected by the Volga River and actually form its channel, their fauna as well as the riverine species of mollusks are included. In a zoogeographic sense, the studied waterways belong to the Euro-Siberian subprovince of the Baltic province. Included is a list of 93 mollusks (58 gastropods, 35 bivalves) that occur in this region. There are two Baltic endemics, *Marstoniopsis steini* and *Anisus vorticulus*; the principle zoogeographic affinities of the other species are delineated.]

ZATRAVKIN, M. N. & V. V. BOGATOV. 1981. Freshwater mollusks of the lower basin of the Amur River. Tez. Doklady k 5-y Vses Limnol. Listvenichnoe na Baikala [Thesis Reports of the Fifth Annual All-Union Society of Limnology. Leaflets on Baikal], Vol. 2, Irkutsk, p. 155.

[Sixty-four species of mollusks, including 12 new species and 4 new records for the Amur Basin were collected in the Nanaysk, Komsomol'sk and Ul'chsk regions of Khabarovsk Territory. Based on these data as well as literature records, the malacofauna includes 69 freshwater species (38 gastropods, 31 bivalves). Distributions of species by geographic areas and types of waterways are examined.]

ZAYKO, V. A. & I. M. ROMANENKO. 1981. Microprobe analyses of the shells of mollusks living in different salinity conditions. BMV 1981(5):74–75 (ES).

[The distribution of chlorine in radial sections of shells of marine, brackish, and freshwater mollusks was studied. The average level of chlorine in shell material increased with an increase in the salinity of the habitat. A correlation was established between seasonal variation in chlorine levels in the shells and salinity of the habitat of corbiculids.]

GASTROPODA, GENERAL PROBLEMS

REX, M. A. & A. WAREN. 1981. Evolution in the deep-sea: taxonomic diversity in benthic gastropods. Biology of the great depths of the Pacific Ocean, Proceedings of the 14th Pacific Science Congress. Khabarovsk. Aug. 1979. Section Marine Biology, Vladivostok, Part 1, pp. 44–49 (ES).

[The taxonomic diversity (average number of species per genus) of deepwater gastropods was studied as an indicator of the degree of adaptive radiation in habitats situated at various depths along the western portion of the North Atlantic. The normalized number of species per genus was lowest on the shelf and increased with depth, reaching its maximum on the continental slope, but again decreased on the abyssal plain. The results presented indicate that gastropods have the highest probability for speciation at bathyal depths (200–4000 m). A less important center of evolutionary radiation occurs at abyssal depths (>4000 m).]

GASTROPODA, PULMONATA, AQUATIC

ALYAKRINSKAYA, I. O. 1981. Adaptation of some freshwater mollusks to conditions in contemporary waterways. ZZ 60(9): 1339–1346 (ES).

[Under similar conditions, *Planorbis planorbis* always contains 2–3 times the amount of hemoglobin found in *Planorbis corneus*.]

ALYAKRINSKAYA, I. O. 1981. Provision of reserve nutrients in the eggs of some gastropods. Doklady AN SSSR [Reports of the Academy of Sciences USSR] 260(1):245–248.

[Levels of albumin in the albuminous fluid of the eggs of *Viviparus viviparus*, *Helix pomatia*, and *Planorbis corneus* were studied quantitatively. Maximum initial concentrations of albumin averaged 37% in *Viviparus*. This was approximately 2.5 times the concentration found in *Helix*, and 4–7 times the concentration in *Planorbis*.]

ARAKELOVA, E. S. 1982. The effectiveness and type of growth in two species of freshwater pulmonate mollusks. ZOB 43(4): [no pagination given] (ES).

[Growth and respiration of juvenile individuals of *Lymnaea ovata* and *Planorbis planorbis* were studied experimentally. Correlations were shown between the rate of growth, shell dimensions, and body mass of these mollusks. Growth rates of juveniles can be approximated by a parabolic function. The coefficient for energy utilization for growth (K_2) was emperically calculated. Growth efficiency decreases in one species, but remains unchanged, or changes insignificantly in the other.]

BEREZKINA, G. V. & YA. I. STAROBOGATOV. 1981. Morphology of the egg capsules of several mollusks of the genus *Lymnaea* (Gastropoda: Pulmonata). ZZ 60(12):1756–1768 (ES).

[The terminology for describing the morphology of egg capsules of freshwater mollusks, especially lymnaeids, is discussed. The term "egg" is applied only to the egg cell with its vitelline membrane, as is accepted in embryology. The egg, surrounded by albuminous fluid and two membranes, is called the "egg capsule." The term "syncapsule" is proposed for a group of egg capsules, immersed in a mucilaginous matrix and completely enclosed in a membrane. The spawn (syncapsules) of 21 species, representing 6 subgenera of the genus *Lymnaea*, are described using this terminology, based on material from Smolensk state. For each species, data on the dimensions of the syncapsule, the number of capsules per syncapsule, as well as the measurements and proportions of the egg capsules are presented. Interspecific differences in the structure of syncapsules and in the dimensions of their elements are noted.]

DAVIDOV, A. F., N. D. KRUGLOV & YA. I. STAROBOGATOV. 1981. Experimental interbreeding of two forms of *Lymnaea stagnalis* with notes on the systematics of the subgenus *Lymnaea s.s.* (Gastropoda: Pulmonata). ZZ 60(9):1325–1338 (ES).

[Conchological analysis of extensive collections of Palearctic representatives of *Lymnaea stagnalis* have shown that they group into six forms, differing, in addition to shell morphology, in distribution and biotope adaptation. Sympatric records (without intergrades) and different distributions in parts of their ranges suggest the presence of six species: *L. fragilis* (L.), *L. stagnalis* (L.), *L. elephila* Kob. non Bgt., *L. doriana* Bgt., *L. media* Hartm. and *L. bodamica* Mill. As a partial test of this hypothesis, experimental crosses of *L. fragilis* × *L. stagnalis* were bred, using a specially developed method. Shell proportions, as well as the morphology and structure of the reproductive system and egg capsules were compared. Results of analyses of F_1, F_2, and F_3 generations showed that in nature, these groups cannot interbreed. American representatives of this group probably belong to five species: *L. occidentalis* Hemph., *L. lepida* Gould, *L. sanctamariae* Walk., *L. jugularis* Say, and *L. stagnalis*, the last introduced into the region of the Great Lakes from Europe. Their systematics requires further careful study of additional material. *Lymnaea s.s.* thus includes a total of 10 Recent species.]

SHAKHMAEV, N. K. 1982. Levels of iron and manganese in the bodies of some mollusks. Khim i biokhim okisl. sistem, sodersh d-elementy (Chemistry and biochemistry of the oxidative system, levels of d-elements) Chelyabinsk, pp. 57–61.

[In an analysis of the levels of iron and manganese in *Lymnaea* and *Planorbis*, the authors found that in the body of the latter, levels of iron are 3–4 times higher, and manganese 2.4 times higher, than in the former. Similarly, the shell of *Planorbis* contains 1.4 times more iron and 1.9 times more manganese than that of *Lymnaea*.]

STADNICHENKO, A. P. & YU. A. STADNICHENKO. 1982. On the molluscan fauna of the *Lymnaea stagnalis* group in the waterways of Crimea. ZZ 61(3):443–445 (ES).

[In the waterways of the Ukraine, there are four described species of the genus *Lymnaea*: *L. stagnalis*, *L. fragilis*, *L. doriana*, and *L. producta*, three of which are widely distributed in the European portion of the USSR. *Lymnaea doriana* is known only from old collections. Only *L. stagnalis* is mentioned in the large body of work on the freshwater malacofauna of the Ukraine. Nevertheless, the study of whorl configuration as well as of a number of other conchological indices confirms these species as separate taxa. In 1949, species of the *stagnalis* group, together with a number of other freshwater mollusks, were introduced to the Crimea from the lower Dnieper River. At the present time, these species have spread beyond the limits of the waterways into which they were originally introduced. It is the opinion of the authors that the *stagnalis* group is represented in Crimea by three distinct species—*L. stagnalis*, *L. fragilis*, and *L. producta*.]

ZAITSEVA, O. V. 1981. Distribution of afferent elements in the central nervous system of pond snails. Arkhiv anatomii, gistol., i embriol. [Archiv for Anatomy, Histology and Embryology] 81(11):35–42 (ES).

[Perfusion with cobalt chloride and horseradish peroxidase aids in determining the distribution of afferent axons and primary sensory cells of the nerves in the cerebral ganglia of the CNS of the mollusk *Lymnaea stagnalis*. Sensory axons pass through the neuropile as well differentiated, strongly localized bundles and form several sensory centers in the ganglia. Numerous sensory filaments extend along the connectives and commissures from the cerebral ganglia to neighboring ganglia on the same and opposite sides of the CNS. A central type of neuropile structure lacking dorsoventral differentiation appears to be characteristic of molluscan Central Nervous Systems.]

GASTROPODA, PULMONATA, TERRESTRIAL

AL'MUKHAMBETOVA, S. K. 1981. Short guide to the *Pupilloidea* (Mollusca: Gastropoda) of the mountain ranges of southern and southeastern Kazakhstan. Izv. AN KazSSR, Ser. Biol. [Proceedings of the Academy of Sciences Kazakhstan SSR, Biology Series], No. 6, pp. 29–32 (Kazakhstani Summary).

[This is a short guide to the pupilloid snails of this area and may be valuable to geologists studying Neogene and Quaternary formations, as well as to parasitologists concerned with the mollusks that are intermediate hosts to trematode worms.]

DMITRIEVA, E. F. & M. MOROZOV. 1981. Effect of methaldehyde on the reproductive activity of the reticulated slug. Nauch. Tr. Leningr. S-Kh. Inta [Scientific transactions of the Leningrad S. Kh. Institute. 405:54–56.]

[Experimental studies have shown that methaldehyde reduces the rate of reproductive development of the reticulated slug, significantly reduces the quantity of eggs laid, increases the speed of their incubation, decreases the percent of young born, and slows their rate of growth.]

GROMOV, A. I., O. A. MONSEEVA, I. V. MALINA, N. V. GROMOVA & S. D. OREKHOV. 1982. Levels of the prostoglandins Fa and E in the tissues of the escargot *Helix pomatia*. ZEBF 18(3): 299–301 (ES).

[Quantitative determinations of levels of the prostoglandins Fa and E in the hemolymph, muscle tissues (caudal portion of the foot), preparations of nerves and buccal ganglia, and also a total nervous system preparation are reported. The highest concentrations are in the nerve tissues. In all cases, levels of prostoglandin E were significantly higher than prostoglandin Fa. These high levels are construed to be indicative of higher intensities of biosynthesis, especially important in the activity of nerve cells. This conclusion is in agreement with the hypothesized role of prostoglandins as regulators of cellular metabolism.]

IL'INSKAYA, O. P. 1981. Morphological and autoradiographic studies on newly formed connective tissue in the vineyard snail. Materialy 12-i Konf. Mol. Uchenykh biol. fak. MGU [Proceedings of the 12th Molluscan Conference, Biology Faculty,

Moscow State University], Moscow. 1981:129–132. Manuscript deposited in VINITI, No. 5484-81 Dep.

[The processes of inflammation and formation of new connective tissue around experimentally introduced foreign bodies (cat gut sutures) were studied in the vineyard snail. The course of the inflammation reaction was followed for periods from 12 h to 15 days after the implantation. There were two morphologically identified cellular elements mediating the reaction: amoebocytes, fulfilling the defense-phagocytic function, and fibroblast-like cells, forming new connective tissue. ^{3}H-thymidine autoradiography showed that these cells have low proliferative activity at the focus of inflammation, and originate from rapidly proliferating precursor cells, located beyond the limits of the focus. These cells, precursors of amoebocytes and fibroblast-like cells, migrate into the site, where their proliferative activity decreases and differentiation is completed.]

Kovalev, V. A., O. V. Zaitseva & V. A. Sokolov. 1982. Investigations of the cerebral portions of the sensory system of the statocysts in pulmonate mollusks. ZEBF 18(4):355–360 (ES).

[The central nervous structures of the statocyst systems on the cerebral ganglia of the pulmonate mollusks *Lymnaea stagnalis* and *Helix vulgaris* were studied in morphological and electrophysiological experiments. By injecting a solution of calcium chloride across the statocyst nerves in both cerebral ganglia, the authors detected several regions of localized neurons that extended their dendrites into the statocyst nerves. Neurons with different types of electrophysiological reactions were found in the zones innervated by these cells. Neurons that did not react to adequate stimulation of the statocysts were also detected. These experiments provided a basis for the assumption that there are no morphological differences distinguishing specific stato-acoustic centers in the cerebral ganglia of pulmonates. Neurons responding to vibrational stimulation, and apparently related to different levels of the sensory system of the statocysts, are situated in different portions of the ganglia.]

Meshkova, N. M. 1982. Changes in body size and protein levels in *Deroceras* (*Agriolimax*) *reticulatum* (Müller, 1774) during growth. Doklady AN SSSR [Reports of the Academy of Sciences USSR] 262(3):740–742.

[Growth of 22 individually maintained slugs was studied under conditions of controlled temperature, humidity, and photoperiod for 6.5 months. Two stages of growth, each with a different average specific rate of growth (srg), occurred in 86% of the individuals. Protein levels in the cells of the reticulated slug were not constant and appeared to be a function of age. The relative quantity of protein in the organism increased from birth to the 75th day of growth, reaching 6.2% (wet weight); after this it gradually decreased to 4.9%.]

Meshkova, N. M., Yu. B. Bysova, M. N. Vilenkina & B. Ya. Vilenkin. 1982. Respiration in growing individuals of *Deroceras* (*Agriolimax*) *reticulatum* (Pulmonata, Agriolimacidae). ZZ 61(8):1148–1153 (ES).

[Body mass and oxygen consumption were measured weekly for each of 23 specimens of *Deroceras reticulatum* that were individually maintained for 200 days, beginning 7–15 days after hatching. The slugs were maintained under conditions of constant temperature, humidity and photoperiod. Statistical analyses of oxygen consumption relative to growth rate showed that the relationship between respiration rate and body mass in growing slugs was more correctly approximated by the linear function $Q = n + mW$, than by the equation $Q = AW^k$.]

Nikolaev, V. A. 1981. Variability and ecology of the enids of the Central Russian Hills. Nauch. Tr. Kursk Ped. In-ta [Scientific Transactions of the Kursk Pedagogical Institute] 210: 54–57.

[Two species of Enidae, *Chondrula tridens* and *Ena obscura,* were found in the study area. The former occurred in two conchological forms, differing in dimensions and degree of development of the apertural armature. The larger form, not commonly found, occurred in more xerothermal conditions with relict vegetation.]

Shapiro, Ya. S. 1981. Estimation of the densities of the slug *Deroceras* (Stylommatophora: Agriolimacidae) in agricultural regions. Nauch. Doklady Vyssh Shk. Biol. N. [Scientific Reports of the Schools for Higher Education in Biological Sciences], No. 10:103–106.

[Studies of criteria for predicting the probability of penetration of introduced species of slugs into agricultural regions, and for estimating their population dynamics were conducted in Leningrad District during the years 1972–1979.]

Tavasieva, T. A. 1982. A new species of gastropod mollusk, *Caucasigena ossetica* n. sp. (Hygromiidae), from the Central Caucasus. ZZ 61(6):938–939 (ES).

[The shell and reproductive system of *Caucasigena* (*C.*) *ossetica,* a new species of hygromiid, are described. The yellowish-white shell is toplike, with a nearly conical contour, and is very similar to the shell of *Stenomphalia selecta.* However, it differs by being larger (major diameter 9–13 mm) and in having an umbilicus that is only slightly covered by the columella. The genitalia contain structural features of both *Kokotschavilia* (form of seminal receptacle) and *Caucasigena* (organization of penial papillae). This species inhabits the Central Caucasus and Northern Osetin, where it is encountered in a variety of habitats at altitudes of 900–2600 m.]

GASTROPODA, PROSOBRANCHIA

Gul'bin, V. V. & M. V. Shul'mina. 1981. Gastropod mollusks from the littoral zone of Sakhalin Island. SID (24):62–74.

[The authors provide a short bibliography and summarize the geographical distribution and ecological characteristics for each of the 43 species found. The zonal-geographic structure of the malacofauna of the entire region is discussed, as are its changes in different parts of the littoral zone.]

Ioganzen [Johansen], B. G. & Ya. I. Starobogatov. 1982. On the discovery of a freshwater mollusks of the family Triculidae (Gastropoda, Prosobranchia) in Siberia. ZZ 61(8):1141–1147 (ES).

[*Sibirobythinella kuznetzkiana,* gen. et sp. nov. is described from the relict "Linden Island" in the foothills of the Kuznetskiy Alatau Mountains [near Stalinsk, western Siberia]. This genus may be readily distinguished from the European *Bythinella* and *Belgrandiella,* which have similar shells, and from the many similar members of the family Triculidae, in which this genus is included, on the basis of radular morphology. This new genus differs from *Pseudobythinella* in having a parietal tooth in the aperture. The issue of uniting the Triculidae and several other closely related families in the superfamily Littoridinoidea is discussed. The presence of relict representatives of the family Triculidae in Siberia and Central Asia, preserved there since the Paleogene, is noted, as is the importance of studying and preserving the relict "Linden Island" fauna in the foothills of the Kuznetskiy Range].

IZZATULLAEV, Z. 1982. Mollusks of the family Bithyniidae (Gastropoda: Pectinibranchia) from Central Asia. ZZ 61(3): 336–340 (ES).

[The genus *Digoniostoma,* hitherto known only from India, southern China, and the Malay Archipelago, is recorded in the freshwater fauna of the USSR. *Digoniostoma oxiana* is described as new and *D. kashmirense,* originally considered a variant from Kashmir, is raised to species status. *Boreoelona caerulans moltschanovi* is added to the fauna of Tadzikistan. Tables for identifications of species are included.]

KANTOR, YU. I. 1982. On the type-species of the genus *Volutopsius* (Gastropoda, Pectinibranchia). ZZ 61(6):843–850 (ES).

[The synonymies of two species of *Volutopsius, V. norvegicus* and *V. largillierti,* both from the northern portion of the Atlantic are critically reviewed. The independence of these closely related species is confirmed based on anatomical data. *Volutopsius largillierti* is the type species of *Volutopsius,* representatives of which are active, selective predators of ophiuroids.]

KONDRATENKOV, A. P. & V. V. KHLEBOVICH. 1981. Dynamics of salinity acclimation and deacclimation of the gastropod mollusk *Hydrobia ulvae.* BMV 1981(4):55–58 (ES).

[*Hydrobia ulvae* acclimates to reduced salinity in 6 days; deacclimation occurs more rapidly than acclimation.]

SERGIEVSKII, S. O. 1982. Ecological studies on the polymorphism of the littoral mollusk *Littorina obtusata* (L.) in the White Sea. Povysh. produktiv. i ratsional. ispol'z. biol. resursov Belogo Morya. Materialy I Koordinats. Sovesh., Leningrad, Mai, pp. 78–79. [Increasing productivity and rational utilization of the biological resources of the White Sea. Materials and Coordinating Conference, Leningrad, May 1982, pp. 78–79].

[The functional significance of polymorphism in *Littorina obtusata,* a common species in the littoral of the White Sea, was investigated, based on approximately 750 samples totaling about 50,000 specimens collected between 1974 and 1981 from different portions of Kandalakshky Bay. Variation in shell color was attributed to three independent loci, with allelic combinations producing over 10 phenotypes. In most populations, 2–3 phenotypes comprised not less than 85% of the variation. Changes in the frequencies of the phenotypes occurred within populations in the absence of isolating barriers. Microgeographic changes were studied in the regions of the Northern Archipelago and of Chupa Inlet. In the former, conditions were fairly uniform, and there was little change in the phenotypic composition of the populations. In Chupa Inlet, two basic trends were evident: (1) in the estuary of the Keret River, there was a sharp increase in the frequency of one of the phenotypes from a normal level of 5–10% to 40–50%; (2) in populations occurring in exposed areas, the degree of polymorphism was significantly higher than in protected ones. Although phenotypes were not affected by trematode infections, both decreased salinity and increased temperature significantly altered the occurrence of different phenotypes. Thus, these data indicate that polymorphism in shell color is adaptive in *L. obtusata.*]

SITNIKOVA, T. YA. & YA. I. STAROBOGATOV. 1982. The extent and systematic status of the group Architaenioglossa (Gastropoda, Pectinibranchia). ZZ 61(6):831–842 (ES).

[A detailed analysis of the homology of the radular teeth of gastropods shows that representatives of the Viviparoidea, the American cyclophorids Neocyclotoidea as well as the Pomatioidea, Valvatidae, Cypraeidae, Ovulidae, and Archimediella possess a specific type of radula, herein called the "archeotaenioglossate." The majority of the representatives of the above groups have a characteristically arranged mantle cavity and pallial oviduct extending from the region of the pericardium. It is proposed that the above enumerated groups be united into the superorder Viviparifomii, with two orders: Cypraeiformes (Cypraeidae and Ovulidae) and Viviparifomes (the other groups). The second of these can be divided into two suborders: Viviparoidei (the majority of the families) and Valvatoidei (Valvatidae). The Old World cyclophorids, including the Cyclophoroidea as well as the Pilidae and Tornidae, are transferred to the order Littoriniformes as representatives having a taenioglossate (but not archeotaenioglossate) radula and the usual mantle cavity morphology. On the basis of the structure of the male reproductive system, the family Viviparidae should be divided into three independent families: Lioplacidae, Viviparidae, and Bellamyidae. The genus *Archimediella* is excluded from the family Turritellidae on the basis of radular morphology and is placed in the independent family Archimediellidae, forming a superfamily in the suborder Viviparoidei.]

VILENKINA, M. N. & B. YA. BILENKIN. 1981. Acclimation and temperature preferences of *Littorina littorea* and *L. obtusata* (Gastropoda: Littorinidae) in the White Sea. ZZ 60(11):1621–1628 (ES).

[Representatives of these snails were collected from the littoral of Kandalak Bay and their temperature preferences and abilities to acclimate to different thermal regimes were investigated.]

BIVALVIA

BELAYEVA, G. G. 1981. Phenoloxidase in the marine bivalves *Crenomytilus grayanus* and *Modiolus difficilis.* ZOB 42(5):771–779 (ES).

[This is the first report and study on the secretions of phenoloxidase by the blood cells of bivalve mollusks. Described are: the participation by the nucleus in the secretion, granulation of the cytoplasm, occurrence of droplets of secretion close to the membrane and in the blood plasma, and mechanisms of secretion, including openings in the membrane and formation of bridges in the cytoplasm. In mollusks, this enzyme can be secreted by all amoebocytes, in contra-distinction, specifically, to insects, in which this function is performed by specialized cells in the blood. It was shown that the variety of forms, structures, dimensions, and colors of amoebocytes may be connected with the process of secreting phenoloxidase.]

BULATOV, K. V. & V. N. IVANOV. 1981. The karyotype of the Black Sea Mussel *Mytilus galloprovincialis* Lam. Tsitol. i Genet. [Cytology and Genetics] 15(6):69–71.

[The chromosome number of the Black Sea mussel from the region of Sevastopol was 2n = 28. The karyotype consisted of 6 pairs of metacentric, 6 pairs of submetacentric and 2 pairs of subteleocentric chromosomes. *Mytilus galloprovinciallis* cannot be distinguished karyotypically from *M. edulis* or *M. californianus* from the Pacific coast of the United States.]

DOTSENKO, B. N., L. N. TROFIMOVA & L. M. L'VOVA. 1982. Experiments on the production of food-stuffs on the basis of the utilization of detritus. Ryb. Kh-vo [Commercial Fisheries], No. 5, p. 41.

[Increase in body mass was studied for 1 month in undetermined species of bivalves mantained in three aquaria, one with detritus, one with detritus and pepsin, and one without detritus. Results showed average growth of 3.4 g in the first, 1.5 g in the second, and 2.8 g in the control. These results suggest the potential use of detritus for the cultivation of bivalves.]

FEDOROV, V. V. & I. A. TSUKUROV. 1981. Environmental studies of the habitat of the littoral scallop by the topographic method. Tez. Vses. Konf. Mol. Uchenykh Posvyashch 60 Letiu Plavmor, Moscow. [Theses of the All-Union Conference of Molluscan Researchers dedicated to the 60th anniversary of the Plavmor Scientific Institute], Moscow, 11–12 April 1981. pp. 29–30. Manuscript.

[A new method for surveying the topography of nearshore regions that conform to the requirements for cultivating scallops is presented, along with results of field and laboratory studies.]

FILATOVA, Z. A. & A. A. SHILEIKO. 1982. Structure and ecology of the deepwater species *Clencharia diaphana* (Clarke, 1961) (Bivalvia: Protobranchia). Byul. Mosk. O-va. Ispit. Prirodi Otd. Biol. [Bulletin of the Moscow Naturalist's Society. Biology Section] 87(2):53–62.

[A functional-morphological analysis of the principal features of the organization of the species, described as *Tindaria* (*Clencharia*) *diaphana,* allows several conclusions to be drawn as to its mode of life. In life, the animals are buried in the upper layer of the bottom sediment, with only the tips of their siphons reaching the surface. Weak development of pedal musculature attests to the poor mobility of this mollusk. Food material, which enters the mantle cavity, is collected by the labial palps from the ctenidia, and possibly, from the inner surfaces of the mantle. The ctenidium, supported by elastic ligaments, serves as the primary water circulating mechanism. When compared with species of the genus *Tindaria,* the independence and distinctness of the monotypic genus *Clencharia* seems clear.]

GABAEV, D. D. & S. M. L'VOV. A collector for artificially cultivating mollusks. [No date given; a patent?]

[A collector for marine scallops is described wherein larvae settle and eventually grow to marketable size.]

KAFANOV, A. I. 1981. Revision of the genus *Ciliatocardium* Kafanov, 1974 (Bivalvia: Cardiidae). SID (24):43–61.

[Seven forms, including *Ciliatocardium ciliatum ochotense,* ssp. nov. and *C. ciliatum nordenskioeldi,* ssp. nov., are added to the Recent fauna. A diagnosis of the genus, including Recent and fossil forms, is provided as are diagnostic tables for all species group taxa.]

KHARAZOVA, A. D. & S. V. FEDOSEEVA. 1981. The effect of salinity changes on protein metabolism in tissues of the edible mussel *Mytilus edulis* from the Sea of Japan. BMV 1981(5): 76–78 (ES).

[Uptake of tritiated glycine in gill epithelium is initially inhibited in reduced salinities but later restored.]

KHARAZOVA, A. D., V. YA. BERGER, V. I. FATEEVA, L. M. YAROSLAVTSEVA & P. V. YAROSLAVTSEV. 1981. Influence of salinity on the dynamics of protein synthesis in isolated gill of Gray's Mussel. BMV 1981(6):56–60 (ES).

[Protein synthesis was investigated in cells of isolated gills of the Gray Mussel *Crenomytilus grayanus* in water with salinities of 6, 16, and 32 ppt (control) by following the incorporation of ^{3}H-leucine. Reversible changes in the rates of protein synthesis occurred in the cells of isolated tissues during adaptation to different environmental salinities. Intracellular levels of free leucine decreased in response to decreasing salinity and were not restored to initial levels within 24 h. It is concluded that cellular mechanisms of adaptation to changing salinities are autonomous.]

KIYASHKO, S. I. & A. A. KARPENKO. 1982. Calcium dependent differences in potential across the mantle of the Giant Oyster. BMV 1982(1):54–56 (ES).

[A calcium dependent difference in electrical potential of 0.6–3.4 mV was found across the mantle of the oyster *Crassostrea gigas.* Electrical properties of the mantle are determined by properties of the shell-producing epithelium.]

KOBLIKOV, V. & I. A. TSUKUROV. 1981. The topography of some regions of Peter the Great Bay (Japan Sea) in regard to the cultivation of the littoral scallop. Tez. Vses. Konf. Mol. Uchenykh Posvyashch 60 Letiu Plavmor, Moscow. [Theses of the All-Union Conference of Molluscan Researchers dedicated to the 60th anniversary of the Plavmor Scientific Institute], Moscow, 11–12 April 1981, pp. 23–24. Manuscript.

[The authors describe the basic physical-geographic conditions suitable for the cultivation of the littoral scallop.]

KORGINA, E. M. 1982. On the movements of *Dreissena polymorpha* Pall. Bio. Vnutr. Vod (Biology of Internal Waters) Leningrad, No. 53, pp. 17–21.

[Under laboratory conditions, dreissenas moved along a horizontal plane at a maximum average speed of 2.1 cm/h for specimens from 11–14 mm in length. They are negatively phototactic and move mostly at night on sandy substrates.]

KOVALEVA, T. A., S. SH. DAUTOV, V. K. KRUCHININ, I. P. SUZDAL'SKAYA & A. V. ZHIRMUNSKII. 1982. Comparative study of contractile properties of adductors in two bivalve species of the family Pectinidae. BMV 1982(1):39–43 (ES).

[The contractile properties of the phase and tonic parts of the adductors of *Swiftopecten swifti* and *Patinopecten yessoensis* were studied, as was the ATPase activity of glycerinated fibers of these muscles. It was found that the phase parts contract nearly 1000 times more rapidly than the tonic. The phase bundles of the adductor muscle of the first species contract more quickly than the corresponding muscle of the second species, although differences in the ATPase activities of their glycerinated fibers were not studied. The tonic parts of the adductor muscles of these species did not differ reliably in the speed of contraction and semi-relaxation, nor in the ATPase activity of the glycerinated fibers.]

KRIVOSHEINA, L. V. & A. L. KOZLYATKIN. 1981. On the distribution of molluscan biotopes in the Bukhtarminsk Reservoir. Fauna i ekol. zhivotnikh Kazakhstana [Fauna and ecology of the animals of Kazakhstan], Alma Ata, pp. 13–21.

[Based on collections made in 1965, 1968, 1970, and 1977, the authors report the occurrence of 55 species of mollusks, and provide details on their depths and substrate preferences as well as on their densities. These mollusks occur most abundantly in the zone of medium depths (4–10 m) and, therefore, are an ideal food supply for fish.]

KULIKOVA, V. A., L. A. MEDVEDEVA & G. M. GUIDA. 1981. Morphology of pelagic larvae of three bivalve species of the family Pectinidae from Peter the Great Bay (Sea of Japan). BMV 1981(4):75–77 (ES).

[Data, including information on shell form, sculpture, and morphology of umbo and hinge, are presented for the larvae of three species of scallops inhabiting Peter the Great Bay (Sea of Japan). The dates of collecting the larvae, the dimensions of the larval shells prior to settling, and the ambient water temperatures are recorded. A diagnostic table distinguishing the larvae is included.]

KUZNETSOV, YU. V. & V. V. DOMASKIN. 1982. Plastic collectors for oyster spat. Ryb. Kh-vo [Commercial Fisheries], No. 5, pp. 32–34.

[Tests conducted in Dzharylgach Bay (Crimea) showed that these

plastic conical cups were effective in collecting oyster spat at densities exceeding 200 spat per cup.]

NISTRATOVA, S. N. & V. I. DANILOVA. 1982. Effects of cyclic nucleotides and 1-methyladenine on the cholinergic cardiac response in bivalve mollusks. ZEBF 18(4):349–354 (ES).

[The effects of cyclic nucleotides and 1-methyladenine on the sensitivities of isolated bivalve hearts to acetylcholine were studied. Cyclic dibutyryladenosine monophosphate, theophylin, papaverin, and NaF produce an accumulation of cyclic AMP within the cell, along with one of two different effects: (1) a significant increase in sensitivity to acetylcholine in the heart muscle of those mollusks with an neurogenic type of choline receptor (*Spisula sachalinensis* and *Callista brevisiphonata*); and (2) a small, lytic effect in those mollusks with tonic (myogenic) choline receptors (*Anodonta* sp., *Crenomytylis grayanus,* and *Modiolus dificilis*). Analogous activity was seen with 1-methyladenine. These data are discussed in the context of possible hormonal influence on the sensitivity to mediators in the reproductive cycle of mollusks.]

ODINTSOVA, T. I., T. M. ERMOKHINA & I. A. KRASHENNINIKOV. 1982. Lysine-rich histones in the mussel *Crenomytilus grayanus.* Biokhimiya (Biochemistry) 47(9):1532–1539 (ES).

[Two lysine-rich histones differing in molecular weight were isolated from mature gonads of mussels. Despite differences in the length of polypeptide chains, these proteins have many similar properties and are highly charged due to high levels of lysine and arginine. Both have levels of arginine, serine, and alanine similar to those in histone H5. Tyrosine residues, which play an important role in the formation of tertiary structure in lysine-rich histones, occupy analogous positions in these two proteins. Spatial organization of the H1 molecule of mussels is identical, indicating that the dimensions and amino acid composition of the globular portions of both proteins are the same. The presence of a globular portion in the lysine-rich histones of mussels confirms the universal tertiary structure of histones H1 and H5. Concentration of all hydrophobic and of the majority of the aromatic amino acids in this portion of the molecule is indicative of its conservatism in amino acid composition, as is the localization of all alpha helices, characteristic features of proteins of this class.]

SARANCHOVA, O. L. & E. E. KULAKOVSKII. 1982. The ecology of the marine starfish *Asterias rubens* L. in connection with the mariculture of the mussel in the White Sea. Povysh. produktiv. i ratsional. ispol'z. biol. resursov Belogo Morya. Materialy I Koordinats. Sovesh., Leningrad, Mai. pp. 74–75. [Increasing productivity and rational utilization of the biological resources of the White Sea. Materials and Coordinating Conference, Leningrad, May 1982, pp. 74–75.]

[The starfish, a serious predator on mussels in the White Sea, frequently completely destroys these mollusks on artificial collectors. One method of control involves placing the artificial substrate in fresh water for 2 h. Mussels tolerate fresh water better than starfish, which die during this exposure.]

SOKOLOV, V. A. & O. V. ZAISTEVA. 1982. Chemoreception in the osphradia of lamellibranch mollusks *Unio pictorum* and *Anodonta cygnea.* ZEBF 18(1):65–70 (ES).

[Preparations stained with methylene blue showed that primary sensory receptor cells are located under the epithelium of the osphradia; peripheral outgrowths of these cells were at the surface of the osphradia, with their central portions in the branchial nerve. Irritation of the osphradium with solutions of NaCl, mannose, glucose, sucrose, and urea produced periodic pulses of activity originating in the visceral ganglion. It is suggested that the osphradial receptors of these mollusks react to changes in the osmotic pressure of the surrounding fluid.]

STADNICHENKO, A. P. 1982. New and little known species of the family *Cycladidae* in the fauna of the Ukraine. Vestnik Zoologiya [Zoological Herald], No. 3, pp. 28–32.

[Data are presented on the distribution and ecology of 13 species of the family Cycladidae new to the fauna of the UkrSSR.]

STADNICHENKO, A. P. & YU. A. STADNICHENKO. 1981. On the influence of larval bitterling on the lamellibranch mollusk *Unio rostratus gentilis* Haas. GZ 17(5):57–61.

[Larvae of the bitterling *Rhodeus sericeus amarus* Bloch develop in the gills of the pearly mussel *U. rostratus,* and are localized in the water tubes of the gills. As the larvae grow, ciliary epithelia of the gill filaments flatten against the walls of the water tubes, and the epithelial cells become shallower, squeezing the blood vessels and connective tissues of the gill. In *U. rostratus* coexisting with *Rhodeus,* there are increased levels of phospholipids in the interfilamental junctions and cells of the connective tissues of the filaments.]

YEFENDIEV, KH. M. 1981. Correlations in the levels of copper, zinc, and lead in the skeletal tissues of Recent and Apsheronian bivalve mollusks. (Topics in Paleobiogeochemistry), Baku, pp. 69–73.

[Using statistical methods, levels of Cu, Zn and Pb were analyzed in Recent members of the genera *Cardium, Didacna, Monodacna, Dreissena,* and *Mytilaster* from different regions in the Caspian Sea, and compared with those of the Apsheronian pelecypods *Monodacna minor, M. laevigata, M. sioegreni, M. pyrophila, Dreissena distincta, D. polymorpha, D. latro, D. eichwaldi,* and *Apsherona propinqua.* Levels of metals increased in the order Cu < Pb < Zn in the shells studied.]

ZATRAVKIN, M. N. 1982. *Unio muelleri* and *Anodonta subcircularis* (Bivalvia: Unionidae) in the delta of the Moscow River. ZZ 61(3):445–447 (ES).

[Specimens of these species were collected at the Moscow State University Research Station near Zvenigorod on the upper part of the Moscow River. Additional samples of *A. subcircularis* were taken from ponds and from the Little Ustre River. Statistical analysis of conchological parameters confirmed the taxonomic status of these species. Further analyses of shell form and periostracum color indicate that *U. muelleri* belongs in the subgenus *Unio* rather than *Tumidusiana.* In the Volga Basin, *Unio* is represented by seven species: *conus, tumidus, muelleri, annulatus, rostratus, limosus,* and *pictorum. Anodonta subcircularis* can be distinguished conchologically, principally by its convexity, from *A. piscinalis.*]

ZHADAN, P. M. & P. G. SEMEN'KOV. 1982. Studies on the function of the abdominal organ in the scallop *Patinopecten yessoensis.* Doklady AN SSSR [Reports of the Academy of Sciences, USSR] 262(1):248–251.

[The function of the abdominal organ of this scallop was investigated in electrophysiological and behavioral experiments. Experiments on isolated preparations showed that the abdominal organ has a high sensitivity to mechanical stimuli, including vibration, and is essentially a mechanosensory structure. Two types of fibers were found reacting to different ranges of vibrations. Vibrational activities at frequencies of 100–600 Hz could be detected.]

CEPHALOPODA

Filippova, Yu. A. & V. L. Yukhov. 1982. New observations on the genus *Alluroteuthis* Odhner 1923 (Cephalopoda, Oegopsida). Antarktika (Antarctica) Moscow, No. 21, pp. 157–168.

[New material, obtained during studies of the diets of sperm whales in the Antarctic, and also during the cruise of the RV *Academicean Knipovich,* provided the first adult individuals of the poorly understood Antarctic squid *Alluroteuthis antarcticus,* previously known only from several juvenile examples. *Alluroteuthis* and the family Neoteuthidae are more precisely diagnosed, and the distribution of this species in the Antarctic region is mapped.]

Khromov, D. N. 1982. A new species of the genus *Sepia* (Cephalopoda: Sepiidae) from the southwestern portion of the Indian Ocean. ZZ 61(1):137–140 (ES).

[*Sepia ivanovi,* sp. nov. is described on the basis of two specimens taken in nearshore waters off eastern Africa. Comparisons are made to closely related species.]

Nesis, K. N. 1982. Zoogeography of the World Ocean: a comparison of pelagic zonation with regional divisions of the shelf (using cephalopod mollusks). "Marine Biogeography, topics, methods, principal divisions" Moscow, 1982, pp. 114–134.

[The basic principles of faunistic and zonal-geographic "regionalization" of the benthic shelf fauna are discussed as are the difficulties of homologizing the zoogeographic provinces of the different oceans and adjacent shores. In an analysis of the distribution of pelagic and shelf cephalopods, an attempt is made to develop a scheme of broad-ranged "regionalization" of the World Ocean and to compare the latitudinal zoogeographic provinces of the shelf against the broad zonality of the pelagic realm. A critically reanalyzed scheme of the zoogeographic provinces (45) of the shelf is presented. The differences in the pelagic fauna of the eastern and western Atlantic, Indo-West Pacific, and eastern Pacific are also analyzed, as are those of the boreal Atlantic and Pacific. The zoogeographic zones of the shelf are compared with the broader pelagic zones. The positions of the Mediterranean, Tasmanian, and South New Zealand province are emphasized. The following regions are recognized on the basis of shelf faunas: Arctic, Atlantic, and Pacific boreal; Western and Eastern Atlantic; Indo-West-Pacific; tropical Eastern Pacific; Magellanic and Kerguelen convergence zone; and Antarctic. They join the Boreal-Arctic, Tropical, and Antarctic super-regions, which correspond to the three larger faunas of pelagic cephalopods].

Nesis, K. N. 1982. Symbiotic bacteria in the reproductive systems of squids and cuttlefish. Priroda [Nature] (1):123–124.

[Accessory nidamental glands (ANG) of loliginid squid, as well as sepiid and sepiolid cuttlefish are white in immature females, but change color, depending on degree of maturity, from yellow and red to coral-red in ripe females. Symbiotic bacteria cause these changes, which are not mediated by hormonal levels in the ovary or by gonadotorpic hormones in the optic glands. The quantity of bacteria increases with the degree of maturity of the female and falls sharply immediately after spawning. The agent responsible for the coloration is called sepiaxanthine. Neither the function of the ANG nor the role of the bacteria is known.]

Nesis, K. N. 1982. Principles of the systematics of Recent cephalopod mollusks. Byul. Mosk. O-va. Ispit. Prirodi. Otl. Geol. (Bulletin of the Moscow Society of Naturalists, Geology Section) 57(4):99–112.

[A survey of the history of the classification and nomenclature of the higher taxa of Recent cephalopod mollusks is presented. From Linnaeus to the present, workers have constantly elevated the ranks of taxa, and there is an exceptionally high number of synonyms of taxa at ordinal rank. The current classification of Recent cephalopods can be considered natural, and contentions about heterogeneity in the orders of squids and octopuses, especially Oegopsida and Incirrata, are unfounded. The ranks reviewed range from the class to the superfamily and the following system is adopted: class Cephalopoda with subclasses Nautiloidea (with a single Recent genus *Nautilus*) and Coleoidea, the latter including four orders: Sepiida with suborders Spirulina and Sepiina; Teuthida with suborders Myopsida and Oegopsida; Vampyromorpha (1 species *Vampyroteuthis infernalis*); Octopoda with suborders Cirrata and Incirrata, the latter divided into three superfamilies: Bolitaenoidea, Octopodoidea, Argonautoidea. The necessity of separating Spirulidae (1 species *Spirula spirula*) as a separate suborder is demonstrated. The phylogenetic position of Vampyromorpha is examined and the inadvisability of maintaining the taxon Decapoda is supported. The entire classification is discussed in the context of the extinct Coleoidea.]

Nigmatullin, Ch. M. 1981. Quantitative aspects of feeding in the squid *Sthenoteuthis oualaniensis* in the Indian Ocean. 4-i S'ezd Vses. Gidrobiol. O-Va. [Fourth Congress of the All-Union Hydrobiological Society] Kiev, 1–4 Dec. 1981. Thesis Report No. 1, pp. 29–30.

[The daily consumption of prey by the oceanic, nectonic squid *S. oualaniensis,* from the equatorial zone of the Indian Ocean was estimated, based on 300 adults, ranging from 15 to 24 cm in length and 150 to 350 g in weight, collected in June–August 1978 in water temperatures of 26–29°C.]

Shchepkin, V. Ya., G. E. Shul'man & A. L. Morozova. 1981. Chemical composition of the tissues of the squid *Sthenoteuthis oualaniensis* (Lesson) from the Red Sea and Indian Ocean. GZ 17(6):61–66 (ES).

[Adult individuals of *S. oualaniensis,* captured in June–August 1978 in the Red Sea and the tropical portion of the Indian Ocean had mantle lengths ranging from 19 to 23 cm and weights between 280 and 540 g. Ninety percent of the females were in the V1–V2 stage of maturity. The liver, mantle, fins, arms, and tentacles were assayed for: levels of dry matter (DM), non-fat dry matter, total lipids (TL), phospholipids, cholesterol, unesterified fatty acids (UEFA), triglycerides, and ethers of cholesterol. Levels of DM in the liver were 1.5–2 times higher than in other tissues, glycogen was twice as high, and TL 3.6–7.5 times as high. The major fraction of TL was in the liver with triglycerides at 53–54%; in the fins and extremities the level decreased to 40–51%. The mass of the liver was, on average, 4.3% of the total mass. High levels of lipids and non-fat dry matter in the liver indicate that the liver plays a role not only in metabolism, but as a reserve, especially of protein and triglycerides. Levels of dry matter, non-fat dry matter, and UEFA in the mantle were higher than in the fins. Levels of lipids and glycogen in the extremities were identical in the arms and tentacles. Swimming in vertical and horizontal migrations utilizes mainly lipids and proteins while rapid swimming consumes glycogen. Levels of glycogen were very low: 10–36 times lower than lipids, and 160–200 times lower than proteins. The squid liver stores very little glycogen. Similarities in chemical composition indicate that food reserves of squid from the Indian Ocean and Red Sea are similar: they are higher than in the Mediterranean *Loligo vulgaris* and lower than reserves of *Todarodes pacificus* from the Sea of Japan and *Illex illecebrosus illecebrosus* from the NW Atlantic.]

Shul'man, G. E., G. I. Abolmasova, A. L. Morozova, Z. A. Muravskaya, A. Ya. Stolbov, V. Ya. Shchepkin & K. K.

YAKOVLEVA. 1981. Physiological and biochemical approaches to ecological studies of the epipelagic squids of the World Ocean. 4-i S'ezd Vses. Gidrobiol. O-Va. [Fourth Congress of the All-Union Hydrobiological Society] Kiev, 1-4 Dec. 1981. Thesis Report No. 3, pp. 134-136.

[The following were studied: (1) The general chemical composition of squid: water content, dry weight, fat, protein, glycogen; (2) fractional composition of lipids: levels of phospholipid, triglycerides, non-esterified fatty acids, cholesterol and its ethers; (3) levels of metabolism: oxygen consumption; (4) production of nitrogen; (5) tissue respiration and respiratory coefficients; and (6) utilization of protein, fat, and glycogen while fasting under experimental conditions. The level of metabolism of the squid *S. oualaniensis* was shown to be very high ($Q = 2.86\ W^{0.78}$). From these data it was determined that the basic energy producing substance in squid is protein, supplemented by triglycerides; glycogen is utilized as an alternate source during stress. By the authors' estimates, the daily reserve ration of a squid is 5-15% of its body mass, the daily growth 1-2%.]

ZUEV, G. V. & M. A. TSYMBAL. 1982. Vertical distribution of the Winged Squid *Stenoteuthis pteropus* (Cephalopoda, Ommastrephidae). ZZ 61(5):683-689 (ES).

[The vertical distribution of the winged squid was determined using data from trawl catches and parameters such as temperature, light, prey supply and levels of dissolved oxygen. Its lower limit of depth distribution is 150-200 m. At night, surface catches decrease 2-3-fold. This squid has different vertical distributions throughout its range, reflecting various oceanographic regimes.]

SCAPHOPODA

CHISTIKOV, S. D. 1982. Recent scaphopod mollusks of the family Entalinidae (Scaphopoda, Gadilida). Report 1. Subfamily Heteroschismoidinae—I. ZZ 61(5):671-682 (ES).

[A preliminary revision of the subfamily Heteroschismoidinae, subfam. nov. (fam. Entalinidae) recognizes three genera: *Heteroschismoides* Ludbrook (1 species), *Spadentalina* Habe (1 species) and *Pertusiconcha*, gen. nov. (2 species—type species *Dentalium callithrix* Dall and contains *P. tridentata*, sp. nov. from the Tasman Sea). The placement of *Entalinopsis* Habe, the type species of which was, apparently, misidentified, is discussed as is the terminology used in the description of the shell and soft parts.]

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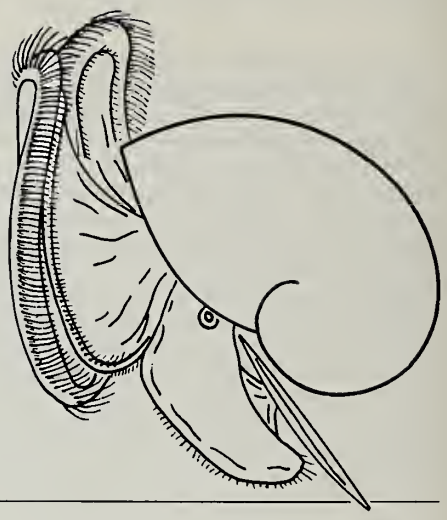

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Information for Contributors

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Cate, J. M. 1962. On the identifications of five Pacific *Mitra.* Veliger 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

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